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Using Herbicides for Reforestation in the Southwest

L. J. Heidmann



Using Herbicides for Reforestation in the Southwest

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ABSTRACT

Site preparation is essential to successfully regenerate conifer stands in the Southwest. Selection of herbicides used to prepare regeneration sites, calibration of equipment, methods of application, and safety are discussed.

FOREWORD

This guide was prepared to assist practicing foresters in the use of herbicides for preparing regeneration areas and releasing trees from herbaceous competition. As such, it does not answer all questions concerning the safe and effective use of herbicides. For information not covered by the guide, the reader is referred to the appropriate state agency which oversees the registration and use of pesticides:

Arizona

State Chemist
P.O. Box 1586
Mesa, Arizona 85201
(602) 833-5442

Colorado

Colorado Department of Agriculture
Division of Plant Industry, Pesticide Inspection
State Services Building
Denver, Colorado
(303) 839-2838

New Mexico

Office of Pesticide Management
New Mexico Department of Agriculture
Box 3AQ
Las Cruces, New Mexico 88003
(505) 646-2133

¹Headquarters is in Fort Collins, in cooperation with Colorado State University. Information reported here was prepared at the Station's Research Work Unit at Flagstaff, in cooperation with Northern Arizona University.

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L. J. Heidmann

INTRODUCTION

To establish most species of trees, some form of site preparation is essential. This is especially true in the southwestern United States, where competing vegetation and deficient and erratic precipitation can effectively prevent establishment of ponderosa pine. Essentially there are three methods of site preparation—chemical, mechanical, and fire. This report discusses techniques for using herbicides to prepare regeneration sites.

Although herbicides are not the solution to all site preparation problems in the Southwest, the use of chemicals has some advantages over other site preparation methods. On areas with dense stands of perennial grass, the mulching effect of the dead vegetation retains more moisture (fig. 1) (Heidmann 1969). Also, because topsoil is not disturbed, the potential for erosion is reduced on steep slopes. Herbicides also may be preferred on terrain unsuitable for mechanical equipment. Some disadvantages of herbicides are that mineral soil is not exposed for natural regeneration, and herbicides may harm people and the environment if not used correctly. It is also sometimes difficult to plant trees on sites where vegetation has been killed by herbicides, especially in heavy brush stands where movement may be limited. An additional disadvantage may be increased fuel loadings and resulting increased fire danger.

Before using any pesticide, the user should have at least an elementary knowledge of laws and regulations pertaining to their use. The term pesticide refers to any

compound for controlling unwanted vegetation, insects, rodents, etc. Herbicides are chemicals used solely for controlling unwanted vegetation, commonly termed weeds.

Federal Laws

In 1910, the first federal law pertaining to pesticides, the Federal Insecticide Act, was enacted. In those days, few pesticides, except for inorganic compounds, were available. Following World War II, with the advent of chlorinated hydrocarbons, the number of pesticides increased greatly. In 1947, Congress passed the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA). This law empowered the USDA to require that manufacturers provide proof of the safety and efficacy of their products, and authorized the Agency to regulate the manufacture and consumer use of pesticides. In 1970, the Environmental Protection Agency (EPA) was created, assuming pesticide responsibility from the USDA. In 1978, FIFRA was amended to assign primary authority for pesticide use enforcement to individual states. Before enforcement authority can legally be transferred by the EPA, however, states must indicate that their regulatory methods will meet or exceed federal requirements.

It is important, therefore, that anyone planning to use herbicides or other pesticides be familiar not only with federal laws, but also with state laws and regulations. In Arizona, for example, all persons working as pesti-

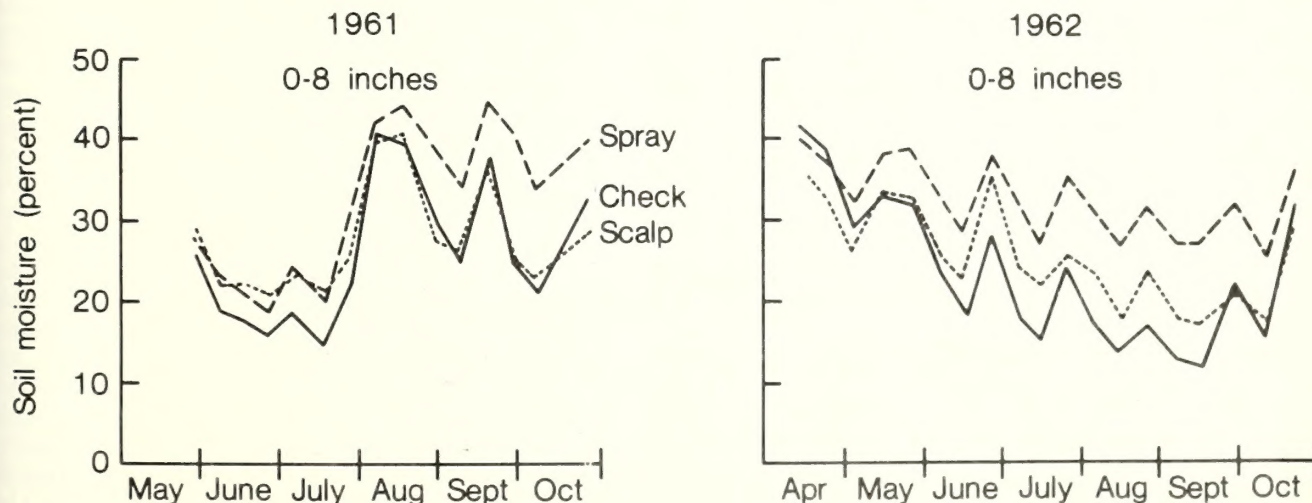


Figure 1.—Percent moisture for the 0- to 8-inch soil depth, under three site preparation treatments, at Wing Mountain, Arizona, in 1961 and 1962.

cide advisors must pass a written general examination on safety, laws, rules, and regulations. In addition, advisors must pass an examination in their particular area of interest. Certification is required to apply restricted use pesticides.

Pesticide Labeling

Anyone working with pesticides should be familiar with pesticide labeling. Labeling refers to the labels and other written, printed, or graphic material which accompanies the pesticide container. The label actually attached to the container may or may not contain all of the necessary information regarding use of the product.

Pesticide labels contain information essential for the safe, effective, and legal use of the product. The label contains the common and chemical names, susceptible species, mixing procedures, season of application, rates, types of equipment to use, the EPA registration number, warnings, and other pertinent information. It is essential that the user read and understand the information on the label before using the product. It is illegal to use any pesticide in a manner inconsistent with its labeling. (Table 1 lists chemical and trade names for some common herbicides used in forestry.)²

Formulations

Liquid herbicides include emulsifiable concentrates and solutions. Dry materials commonly used are dusts, granules, and soluble and wettable powders. It is important to determine the formulation to be used, because it

²Mention of a trademark or proprietary product name does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products that may also be suitable.

may dictate the choice of equipment. For example, wettable powders are finely divided particles which form a suspension when mixed with water. The spray mixture must be agitated constantly during use; therefore, a sprayer with this capability is required.

CLASSIFICATION OF HERBICIDES

General and Restricted Use

Herbicides may be classified in several ways. The 1972 amendment to FIFRA empowered the EPA to classify all herbicides as general or restricted use. The most important restricted use herbicides for forestry are picloram and paraquat, which may be used only by or under supervision of certified personnel. Some herbicides have been removed from the forestry market (e.g., 2,4,5-T). To determine whether an herbicide is approved for use in a particular area, consult with the proper state agency.

Plant Responses

Herbicides can also be classified as selective and nonselective. The term "selective" implies that target plants are killed, but desirable plants are not. This may or may not be true. Nonselective herbicides are intended to kill all of the vegetation on the site. Certain herbicides, however, may fit into both categories. Simazine, for example, may be used selectively to kill unwanted vegetation in citrus orchards and nonselectively to control weeds along fences and on other noncrop sites. Usually, the difference between selectivity and nonselectivity is in the dosage, the placement, and the timing. Some herbicides may be highly selective in pine plantations at rates of 5 pounds per acre, whereas 50 pounds per acre will kill all vegetation present.

Table 1.—Trade and chemical names of some commonly used forestry herbicides

Trade name	Common chemical name of active ingredient	Chemical name
Dowpon M Aatrex 80 W	Dalapon Atrazine	2,2-dichloropropionic acid 2-chloro-4-ethylamino-6-isopropylamino-s-triazine
Esteron 4 Roundup	2,4-D Glyphosate	2,4-dichlorophenoxyacetic acid isopropylamine salt of N-(phosphonomethyl) glycine
Milogard Princep Asulox Goal	Propazine Simazine Asulam Oxyfluorfen	2-chloro-4,6-bis (isopropylamino)-s-triazine 2-chloro-4,6-bis(ethylamino)-s-triazine methyl sulfanilylcarbamate 2-chloro-1-(3-ethoxy-4-nitrophenoxy)-4-(trifluoromethyl) benzene
Modown	Bifenox	methyl 5-(2',4'-dichlorophenoxy)-2-nitrobenzoate
Spike	Tebuthiuron	1-(5-tert-butyl-1,3,4-thiadiazol-2-yl)-1,3-dimethylurea
Tordon Velpar	Picloram Hexazinone	4-amino-3,5,6-trichloro-picolinic acid 3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)dione

Selective and nonselective herbicides work either through the foliage or the roots. Foliage-applied herbicides act in two ways. Systemic herbicides are absorbed by the foliage and translocated within the plant's vascular system to the site of action. Because the herbicide is translocated throughout the entire plant, the entire plant can be killed, although some systemics do not enter the roots. Systemic herbicides generally must be applied when the plant is actively growing and the foliage is green. Contact herbicides kill only the plant parts actually contacted and have little movement within the plant. Contact herbicides, therefore, must be applied in enough carrier (usually water) to adequately cover the foliage. Dalapon and 2,4-D are examples of foliage-applied systemic herbicides which are selective; amitrole is nonselective. Bromoxynil is a selective foliage-applied contact herbicide; paraquat is a nonselective one.

Soil-applied herbicides must be moved into the soil by water or mechanical incorporation. Most soil-applied herbicides used in forestry are known as preemergents. That is, they are applied to the soil in the fall or winter and kill grasses or forbs after the seeds germinate, the following spring and summer. Atrazine is a selective soil-applied herbicide which is translocated in the plant; trifluralin is a selective soil-applied herbicide which is generally nonmobile. An example of a nonselective soil-applied herbicide is methyl bromide, which is used as a soil sterilant.

DOING THE JOB

Selecting the Herbicide

The herbicide selected for a particular weed and crop problem should be recommended for the specific pest by proper authorities. Safety should be considered also. For example, an herbicide may be available in both a granular and wettable powder form. If drift is a matter of concern, it may be advisable to use the granular material.

If an area to be planted is devoid of trees and covered with a mixture of perennial grasses, sedges, and forbs, then a nonselective herbicide, such as glyphosate (Roundup), or a mixture of the selective herbicides dalapon and atrazine may be used. If advanced regeneration is present, glyphosate should not be used unless it can be applied as a directed spray, avoiding conifers. Dalapon usually can be broadcast sprayed where conifers are present, if the trees are several years old and mild surfactants (wetting agents) are used. However, dalapon may damage ponderosa pine and other conifers, under certain situations. Work conducted in the Pacific Northwest has shown that combinations of dalapon and atrazine are more effective in controlling grasses and forbs than either herbicide alone, and are less toxic to conifers (Newton and Overton 1973, Dimock and Collard 1981). Asulam is quite effective on forbs and bracken fern. Ferns are usually found on moister sites, typical of mixed conifer and spruce-fir forests. Two

newer herbicides, oxyfluorfen and bifenox, are quite effective on forbs and annual grasses. At present, however, these herbicides are registered only for nursery use.

Control of brush species, such as New Mexican locust and Gambel oak, with herbicides is difficult because of the tendency for these species to sprout. Prior to 1979, the most widely used herbicide for brush control was 2,4,5-T. The use of this herbicide is now mainly suspended. There are herbicides, such as picloram, which will control brush, but they persist in the soil for extended periods of time, thus making it difficult to plant pine trees. It may be possible to control brush by burning it and spraying the sprouts when they appear. Two of the newer herbicides which hold promise for brush control are tebuthiuron and hexazinone. Tebuthiuron, however, can be applied in Arizona, only by representatives of the manufacturer (Elanco). Table 2 lists some suggested herbicides to use in various cover types.

Factors Affecting Rates

The amount of herbicide to use varies with vegetation being controlled, soil texture, organic matter, and precipitation. An elementary knowledge of soils is helpful in planning herbicide projects. In a clay soil, for example, more herbicide is necessary to control the vegetation than on a sandy soil (table 3), because cations in the herbicidal solution bind to negatively charged clay soil particles. In addition, finer textured soils (silts and clays) generally have greater microbial activity because of increased amounts of organic matter, which results in a faster breakdown of the herbicide. In sandy soils, there is less microbial activity and, consequently, less breakdown of the herbicide. Herbicides leach from sandy soil faster than from clay, but if precipitation is deficient after herbicides are applied, they may remain in the soil for a considerable period of time without breaking down. If this is the case, herbicides such as dalapon, which are usually nontoxic to conifers, may be absorbed by the tree roots and translocated to the tops (fig. 2). Herbicide rates, therefore, should be adjusted accordingly to suit the soil texture. As an example, atrazine is used at rates of 10 pounds of active ingredient or more for controlling forbs and annual grasses on basalt-derived soils which are high in silt and clay content. On agricultural areas in the Southwest, where soils often are quite sandy, atrazine is used at rates of 1-2 pounds per acre. Information on rates for various soils is on the herbicide label.

Adjuvants and Surfactants

Materials added to an herbicide to improve its action are called adjuvants. They may already be included in the product or may be added separately before use. Adjuvants include surfactants, emulsifiers, thickening or sticking agents, penetrating agents, and dispersing agents. They may greatly increase the effectiveness of an herbicide but also reduce its selectivity.

Table 2.—Suggested herbicides for preparing coniferous regeneration sites in the Southwest

Predominant cover	Herbicide (common name)	Application rate (pounds ai/acre) ^a	Season of application or foliage condition
Perennial grass	Dalapon	5-10	actively growing
	Glyphosate	2-4	actively growing
Perennial grass and forbs	Dalapon	5-10	actively growing
	plus Atrazine	4-10	
	Glyphosate	2-4	actively growing
Perennial grass and advance regeneration or, perennial grass, forbs, and advance regeneration	Dalapon	5-10	actively growing
	plus Atrazine	4-10	
	Glyphosate	2-4 ^b	actively growing
Annual grass and forbs, or forbs, annual grass and advance regeneration	Atrazine	4-10	fall, winter
	Simazine	4-10	fall, winter
	Asulam	2-4	summer
	Oxyfluorfen ^c	1/2-1	spring, summer
	Bifenox ^c	2-4	spring, summer
Bracken fern	Asulam	3-7	summer
Brush	Hexazinone	1-2	summer
	Picloram	75-85 ^d	early spring
	Tebuthiuron	1/2-2	summer

^aRate will depend upon species of vegetation and soil type. Consult label for more detailed information.

^bDo not use glyphosate in newly established plantations. Underspray larger trees being sure to avoid conifer foliage.

^cNursery use only.

^dPounds of product (Tordon K pellets). Restricted use herbicide.

Table 3.—Soil characteristics for various soil types

Characteristic	Sand	Loam	Clay	Peat/Muck
Absorption capacity	very low	low	moderate	very high
Herbicide leachability	rapid and deep	moderate	low	almost none
Relative herbicide activity	high	moderate	moderate to low	very low



Figure 2.—Example of herbicide damage in larger trees. Dalapon was applied the preceding summer, but because of dry winter conditions and a sandy soil, the herbicide did not break down. Left photo was taken in June 1977, about 1 year after treatment. Right photo, showing recovery, was taken in November 1977.

Surfactants accentuate the emulsifying, spreading, or wetting properties of a spray solution at a surface. They work by reducing the surface tension of water thus allowing the solution to flow over or wet the plant leaf more thoroughly. The result is that more of the herbicide is able to enter the plant.

Surfactants can be grouped into three categories according to electrical charge:

Type	Charge
Anionic	Negative
Cationic	Positive
Nonionic	Neutral, no charge

The nonionic surfactants are most commonly used in agricultural sprays, because they are relatively unaffected by water hardness.

Application Methods and Equipment

Ground Rigs

Commercial sprayers used in agriculture have essentially the same design (fig. 3). The basic components are a tank, pump, hoses, pressure regulator, and a boom with nozzles. To resist the corrosive effect of most agricultural chemicals, the tank should be constructed of stainless steel or fiberglass-reinforced plastic. Agitation is necessary in most spray tanks. Bypass, or hydraulic agitation is adequate for compounds forming true solutions or for emulsifiable formulations. High pressure jet or mechanical paddle agitation is essential to maintain adequate mixing of wettable powders, flowable liquid concentrates, and emulsions containing much oil.

The pump provides the necessary pressure to force the solution through the hoses and nozzles. There are several types of pumps, but the most versatile is the piston pump. It operates over a wide pressure range, is resistant to wear from abrasive materials—such as wettable powders, and has a long service life. The main disadvantage is a low flow rate, which means that the tank must have mechanical agitation.

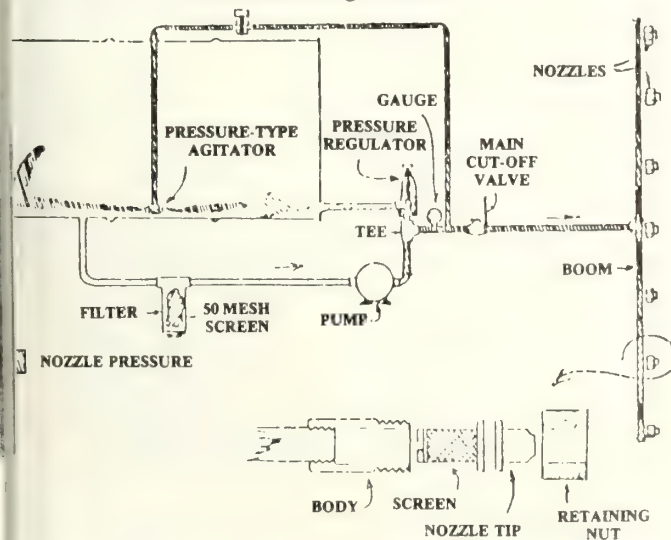


Figure 3.—Schematic drawing of basic components of a sprayer.

A pressure regulator is needed to maintain a constant pressure in the system to keep the amount of material applied uniform. Excess solution is routed back from the pressure regulator relief valve into the spray tank. Control valves are needed between the pressure regulator and the boom.

Hoses and lines must be able to withstand the chemicals or the carriers used, especially petroleum solvents. A coarse strainer should be used for filling the tank. In-line strainers between the tank and the pump, as well as behind each nozzle, should be used. Screens should not be finer than 50 mesh for wettable powders, but can be 100 mesh for emulsions and true solutions. Booms can vary from a few feet to more than 70 feet in length. However, to get uniform coverage, the pressure at each nozzle needs to be the same, and the height of each nozzle above the ground needs to be uniform. For wide swaths, boomless jet nozzles which cover strips up to 60 feet wide may be used (fig. 4). The most common jets and nozzles used in commercial sprayers give flat, fan shaped or conical patterns.

Aerial Application

On areas larger than 100 acres, it may be less expensive to apply herbicides by air (fig. 5). Much of the cost, however, depends on deadhead time (time involved in flying from the base to the spraying site). If the aircraft can land adjacent to the site, costs will be less than if several minutes are required to return to the base for each load.

Aerial spraying is best suited to level terrain free of standing obstacles. In much of the Southwest, fixed wing aircraft cannot be used because of steep slopes and canyons. Helicopters are effective over much of this terrain but are more expensive to operate. Aerial application gives rapid coverage of the area and thus may be less expensive. However, there are some disadvantages to aerial application. Drift is more of a problem, and hazards to the applicator are greater than to operators of ground equipment because of terrain and standing obstacles.

Backpack or Hand-held Equipment

For spraying smaller areas or doing "touchup" spraying, different types of smaller sprayers are available. The micron sprayer (fig. 6) is ideal for spraying small acreages. It consists of a battery-operated motor which spins a small disk, producing very small uniform droplets. The tank only holds 2.5 liters of solution, but because of the very fine spray applied, this is sufficient to cover approximately 0.6 acre. One person can spray several acres a day with a micron sprayer. A disadvantage of the micron sprayer is that it puts out a circular spray pattern about 5 feet in diameter. It is sometimes difficult to spray around and between individual trees with this type spray pattern. Another sprayer which uses more material but is useful for spraying small areas is typified by the Solo model 425 backpack

pressure sprayer (fig. 7). With a flat spray nozzle, a spray solution can be directed right up to the base of small seedlings without getting material on the foliage. This sprayer, however, holds only 3 gallons of solution, which limits its usefulness to small areas.

The backpack mistblower is another sprayer suited for smaller spraying jobs (fig. 8). Because of the small droplet size, about 8 to 10 gallons of solution will treat 1 acre. A major disadvantage is that because of the weight and the vibration from the running motor, it is difficult for one individual to work with the mistblower for long periods of time. It is much more tiring than the micron sprayer or the backpack pressure sprayer.

Granular Application

Many herbicides are available in granular form and are applied dry, generally to control unwanted trees and brush. Often, the material may be broadcast under individual trees by hand. When applying granular material in this manner, the applicator must be certain to wear rubber gloves and a respirator. Granular material also may be broadcast with "cyclone seeders" or may be applied by air.

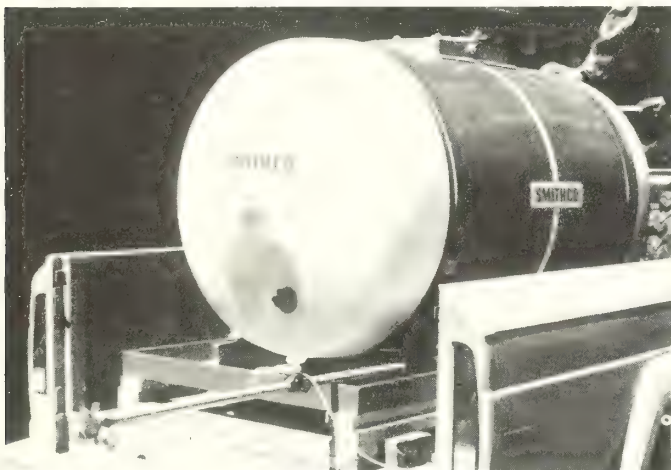


Figure 4.—Truck mounted pressure sprayer with a boomless jet capable of spraying a 50- to 60-foot swath.



Figure 5.—Large acreages can be sprayed most economically by aircraft.



Figure 6.—The "Herbi" micron sprayer. The 2.5-liter bottle contains enough spray solution to cover about 0.6 acre.

Mixing the Spray Solution

As an example, assume the task is to spray a 50-acre parcel which has a dense cover of Arizona fescue and mountain muhly. Previous experience has shown that a rate of 5 pounds of active ingredient (a.i.) per acre of the magnesium salt of dalapon (Dowpon M) will effectively control these two species on a clay loam soil. In some instances, when perennial grasses are controlled, a site may be invaded by forbs and annual grasses the following year. Because of this, a preemergent herbicide should be added to the spray mixture. Based on previous research, 5 to 10 pounds a.i. of atrazine or simazine per acre probably will be needed. Also, 40 gallons of spray solution per acre is necessary to provide good coverage of the grass species, if the material is applied with ground equipment. The solution can be prepared as follows:

Dalapon Five pounds a.i. of the magnesium salt per acre sprayed are needed. Dowpon M is 84.5% active ingredient; therefore, divide 5 pounds by 0.845, resulting in 5.92 pound (5 pounds 14.7 ounces) of the product (Dowpon M) needed per acre.

Atrazine Ten pounds a.i. atrazine per acre is needed. Using commercial Aatrex 80 W, which contains 80% a.i., divide 10 by 0.8 to determine that 12.5 pounds (12 pounds 8 ounces) of the product is required per acre.

Surfactant The average amount of surfactant used in most herbicide sprays is approximately 0.125% to 0.5% (1 pint to 2 quarts per 100 gallons of spray solution). The maximum effect obtained with a given concentration will vary with surfactant and herbicide. Phenoxy-type herbicides (e.g., water soluble amine of 2,4-D) generally show maximum increases around 0.2% to 0.5%, while other types of foliar-applied herbicides (dalapon, paraquat, amitrole, etc.) often show maximum effects from 0.5% to 1.0%. For the surfactant, 0.5% of Tween 20 will be used here. This means that 0.2 gallon (758 cc) of Tween is needed for each 40 gallons of solution.



Figure 7.—A backpack pressure sprayer suitable for treating small areas.



Figure 8.—A backpack mistblower. The tank holds enough solution to spray approximately one-third acre.

The herbicides and wetting agent are added to water to give a total solution of 40 gallons per acre sprayed. On the 50-acre plot, the following will be needed:

- 296 pounds of dalapon—(5.92 pounds product per acre \times 50 acres)
- 625 pounds of atrazine—(12.5 pounds product per acre \times 50 acres)
- 10 gallons of Tween 20—(50 acres \times 40 gallons per acre \times 0.05%)
- 2,000 gallons of water—(50 acres at 40 gallons per acre).

Calibration

Calibration ensures that the proper amount of spray solution is applied to the site. There are three acceptable methods for calibrating sprayers: by varying the speed of the sprayer, by varying the pressure, and by varying the nozzle size.

Adjusting the Pressure

Beginning with the assumptions that experience indicates the best speed for driving the spray rig is 3 miles per hour (264 feet per minute), and that the available equipment is a boomless jet which gives a spray width of approximately 60 feet, the pressure needed can be calculated. In 1 minute, 15,840 square feet will be covered (264 feet \times 60 feet). To spray 1 acre, therefore, will take 2 minutes 45 seconds (43,560 square feet/15,840 square feet = 2.75 minutes = 2 minutes 45 seconds). Because it is necessary to apply 40 gallons of solution per acre, a discharge rate of 14.55 gallons per minute (40 gallons/2.75 minutes = 14.55 gallons) is needed. To find out the actual discharge rate of the equipment being used, fill the spray tank with clean water and turn on the sprayer. Collect and measure the amount of water discharged in a specified period of time (e.g., 30 seconds). Do this at least three times to get an average figure. It is found that the sprayer is discharging 10

gallons per minute. Because a discharge rate of 14.55 gallons per minute is needed, it is necessary to adjust the pressure regulator until the proper discharge is attained. Changing the pressure is not advisable for making gross changes in discharge, however, because a pressure change may change the nozzle pattern and droplet size. Pressure must be increased four times to double the output.

Adjusting the Speed

In the above illustration, the sprayer, before adjustments, delivered 10 gallons per minute which would require 4 minutes to spray each acre (40 gallons/10 gallons per minute). The sprayer will need to cover 10,890 square feet per minute at this discharge rate (43,560 square feet/4 minutes). Because the swath width is fixed at 60 feet (for this particular boomless jet), it is necessary to travel 181.5 feet per minute to cover 10,890 square feet (10,890/60). This is a speed of slightly more than 2 miles per hour. A slower speed means more material delivered.

Changing Nozzle Tips

The amount of spray discharged is related to the size of the opening in nozzle tip. A larger opening will deliver more spray solution at the same speed and pressure than a smaller one. A TeeJet 8001E spray tip, for example, delivers 0.10 gallon per minute at 40 pounds pressure, while a 8015E tip delivers 1.50 gallons per minute at the same pressure. Adjusting nozzle tips is the best method for making gross changes in the delivery rate.

When using hand-held equipment for spraying small areas, it is difficult to apply solutions uniformly, because the sprayer may be held in one location for too long or too short a period, or the speed at which the person walks may be uneven. To overcome this problem, it is necessary to accurately calibrate the sprayer and to make sure that application is uniform. The applicator should determine the specific distance to be covered in a specified period of time to apply the desired amount of material. After this has been determined, practice by walking a specified distance in a specified period of time with the sprayer. If, for example, it has been decided that a strip 10 feet wide and 100 feet long has to be covered in 2 minutes with a mistblower to apply dalapon at a rate of 5 pounds of active ingredient per acre, the applicator should practice walking this strip with the sprayer until the timing is correct.

SPRAYING CONDITIONS

Spraying should not be attempted in windy conditions. Usually for ground spraying, the winds should be less than 10 miles per hour and for aerial application less than 5 miles per hour. Spraying conditions are usually best in early morning or late afternoon and evening,

when winds tend to be moderate. In addition, at these times, stomata are more likely to be open, which enhances the uptake of herbicides. Systemic herbicides usually are less effective when plants are under stress because the stomata are likely to be closed.

The most appropriate time to apply systemic herbicides in the Southwest is during the summer rain season. Herbicides such as dalapon may be applied on days when it rains, if the spraying can be done a couple of hours before rains begin.

SAFETY IN USING HERBICIDES³

Safety in using herbicides is related chiefly to effect on humans, nontarget plants, and other life forms.

Human Safety

Herbicides are classified into four toxicity classes, as determined by the LD₅₀ values, which are expressed in milligrams of orally administered herbicide per kilogram of body weight that results in killing 50% of test animals. Herbicides may also be toxic if inhaled or absorbed through the skin. Table 4 lists the four toxicity classes, along with some examples and the amount of material considered to be a lethal dose to a 160-pound person.

Herbicides are relatively low in toxicity to humans compared to other pesticides. Most herbicides present no particular hazard when handled with reasonable care and applied in accordance with registered and recommended uses. One exception, however, is methomyl, a highly poisonous gas widely used as a soil fumigant in tree nurseries. Specific precautions and handling instructions on herbicide labels should always be followed.

Good handling habits must be encouraged and practiced with all pesticides. Personnel should be trained and supervised to prevent unnecessary exposure. Specific allowable herbicide residues (tolerances) are established by EPA. These residue tolerances are premised on the protection of human welfare. Registered herbicides and recommended application rates should be strictly observed to avoid the possibility of excessive (illegal) residues. Spray drift from one crop to another or from noncrop areas to crop areas should be avoided to prevent illegal residue and/or crop injury.

Protection of Nontarget Plants

The greatest hazard associated with herbicides is the phytotoxic effect on nontarget plants caused by incorrect or inaccurate application. Spray drift in either particle or vapor form, soil contamination resulting in subsequent root uptake by nontarget plants, excess

³Taken from *Study Guide for Agricultural Pest Control Advisers*, William Finch, editor. Arizona Agricultural Chemicals Association, Phoenix (Revised 1980).

Table 4.—Pesticide toxicity classes and LD₅₀ values for some common materials

Toxicity Class	LD ₅₀	Required on label	Examples	Amount required to kill 160-pound individual		
				LD ₅₀		
	<i>mg/kg</i>			<i>mg/kg</i>	<i>gm</i>	<i>ounces</i>
Highly toxic	1-50	Danger, Poison, Skull and Crossbones KEEP OUT OF REACH OF CHILDREN	Methyl bromide	35	2.54	0.09
Moderately toxic	50-500	Warning! KEEP OUT OF REACH OF CHILDREN	2,4-D	300	21.77	0.77
				1,000	72.57	2.56
			2,4,5-T	481	34.91	1.23
			Paraquat	157	11.39	0.40
Slightly toxic	500-5,000	Caution, KEEP OUT OF REACH OF CHILDREN	Aspirin	1,200	87.09	3.07
			Atrazine	3,000	217.72	7.68
			Cacodylic acid	830	60.24	2.12
			Simazine	5,000	362.87	12.80
Practically nontoxic	Above 5,000	KEEP OUT OF REACH OF CHILDREN	Picloram	8,200	595.11	20.99
			Dalapon	9,330	677.12	23.88
			Amitrole	24,600	1,785.33	62.98

oil persistence causing injury to subsequent crops, and prayer contamination are to be avoided. Plant growth regulators (hormone-like herbicides) present the greatest visible hazard to nontarget plants, principally to the broad-leaved group, through drift. Herbicides may be subject to drift for considerable distances. Also, many herbicides are mobile in the soil. Therefore, caution should be exercised when spraying near bodies of water or on steep slopes.

Other Environmental Effects

At normally recommended rates, herbicides generally do not pose a hazard to livestock or wildlife. Herbicides are relatively nontoxic to honey bees. Herbicides often can be used to benefit wildlife by manipulating vegetation and improving habitat. Reduction of dense brush and aquatic weeds are examples of environmental enhancement.

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GLOSSARY³

- Absorption**—The process by which herbicides are taken into plants by roots or foliage (stomata, cuticle, etc.).
- Acid equivalent (ae)**—The theoretical yield of parent acid from the active ingredient content of a formulation.
- Active ingredient (ai)**—The agent in a product primarily responsible for the intended herbicidal effects, and which is shown as the active ingredient on the herbicide label.
- Broadcast application**—Herbicide treatment over an entire field area.
- Brush control**—Control of woody plants such as brambles, sprout clumps, shrubs, trees, and vines.
- Carrier**—A gas, liquid, or solid substance used to dilute or suspend an herbicide during its application.
- Compatibility**—Ability to mix in the formulation or in the spray tank for application in the same carrier without undesirably altering the separate characteristics or effects of components.
- Concentration**—The amount of active ingredient or herbicide equivalent in a quantity of diluent expressed as percent, lb/gal, ml/liter, etc.
- Contact herbicide**—An herbicide that causes localized injury to plant tissue with which it comes into contact.
- Diluent**—Any gas, liquid, or solid material used to reduce the concentration of an active ingredient in a formulation.
- Directed application**—Precise application to a specific area or plant organ, such as to a row or bed or to the leaves or stems of plants.
- Emulsifiable concentrate (ec)**—A single-phase liquid system, having the property of forming an emulsion when mixed with water.
- Emulsifying agent (or emulsifier)**—A substance which promotes the suspension of one liquid in another.
- Emulsion**—One liquid suspended as minute globules in another liquid (for example, oil dispersed in water).
- Encapsulated formulation**—Herbicide enclosed in capsules (or beads) of thin polyvinyl or other material, to control the rate of release of the chemical and extend the period of diffusion.
- Flowable formulation**—A two-phase concentrate that contains solid herbicide suspended in liquid which is capable of suspension in water.
- Foliar application**—Application of an herbicide to the leaves or foliage of plants.
- Formulation**—(1) An herbicide preparation supplied by a manufacturer for practical use; (2) the process, carried out by manufacturers, of preparing herbicides for practical use.
- Fumigant**—Chemical used in the form of a volatile liquid or gas to kill insects, nematodes, fungi, bacteria, seed, roots, rhizomes, or entire plants; usually applied in an enclosure of some kind or in the soil.
- Granular**—A dry formulation of herbicide and other components in discrete particles generally less than 10 mm³ in size.
- Herbaceous plant**—A vascular plant that does not develop persistent woody tissues above ground.
- Herbicide**—A chemical used to control, suppress, or kill plants, or severely interrupt their normal growth processes.
- Hormone**—A growth-regulating substance occurring naturally in plants or animals; also refers to certain man-made or synthetic chemicals with growth-regulating activity. These, however, are more correctly called synthetic regulators; they are not hormones.
- LD₅₀**—The dose (quantity) of a chemical calculated to be lethal to 50% of the organisms in a specific test situation, expressed in weight of the chemical (mg) per unit of body weight (kg); the toxicant may be fed (oral LD₅₀), applied to the skin (dermal LD₅₀), or administered in the form of vapor (inhalation LD₅₀).
- Nonselective herbicide**—A chemical that is generally toxic to plants without regard to species. Toxicity may be a function of dosage, method of application, etc.
- Noxious weed**—A weed specified by law as being especially undesirable, troublesome, and difficult to control; definition varies according to legal interpretations.
- Organic matter**—That organic fraction of the soil which includes plant and animal residues at various stages of decomposition.
- Pellet**—A dry formulation of herbicide and other components in discrete particles, usually larger than 10 mm³.
- Pesticide**—Any substance or mixture of substances intended for control of insects, rodents, fungi, weeds, and other forms of plant or animal life that are considered to be pests.
- Phytotoxic**—Injurious or lethal to plants.
- Plant growth regulator**—A substance used to control or modify plant growth processes without appreciable phytotoxic effect at the dosage applied.
- Postemergence (POE)**—Applied after emergence of the specified weed or planted crop.
- Preemergence (PE)**—Applied prior to emergence of the specified weed or planted crop.
- Rate**—Amount of active ingredient or acid equivalent applied per unit area or other treatment unit.
- Residue**—That quantity of an herbicide remaining in or on the soil, plant parts, animal tissues, whole organisms, and surfaces.
- Selective herbicide**—A chemical that is more toxic to some plant species than others.
- Spot treatment**—Herbicide application over small, restricted areas of a whole unit (i.e., treatment of spots or patches of weeds within a larger field).
- Spreader**—A material which favors or improves the emulsifying, dispersing, spreading, wetting, or other surface-modifying properties of liquids; often used interchangeably with surfactant.
- Surfactant**—A material which favors or improves the emulsifying, dispersing, spreading, wetting, or other surface-modifying properties of liquids.
- Suspension**—Mixture containing finely divided particles dispersed in a solid, liquid, or gas.
- Systemic herbicide**—A compound that is translocated within the plant and has an effect throughout the entire plant system.

ank-mix combination—Mixing of two or more pesticides or agricultural chemicals in the spray tank at the time of application.

olerant—Capable of withstanding effects; for example, grass is tolerant of 2,4-D to the extent that this herbicide can be used selectively to control broad-leaved weeds without killing grass.

oxicity—The inherent capacity of a substance to produce injury or death.

ranslocated herbicide—An herbicide that is moved within the plant; translocated herbicides may be either phloem mobile or xylem mobile, but the term is frequently used in a more restrictive sense to refer to herbicides that are moved in the phloem.

ater dispersible granule—A granular, dust-free wettable powder formulation which, when suspended in water, will require agitation.

Water soluble concentrate (wsc)—Forms a true solution in water (like a water soluble powder), thus requiring little agitation.

Water soluble powder (sp)—Dissolves in water to form a true solution; requires little agitation or mixing.

Weed—A plant growing where it is not desired; plants are considered weeds when they interfere with activities of man or his welfare.

Wettable powder (wp)—A finely divided, dry formulation that can be readily suspended in water.

Wetting agent—Substance which serves to reduce interfacial tensions and causes spray solutions or suspensions to make better contact with treated surfaces (see surfactant).

Pesticide Precautionary Statement

Pesticides used improperly can be injurious to man, animals, and plants. Follow the directions and heed all precautions on the labels.

Store pesticides in original containers under lock and key—out of the reach of children and animals—and away from food and feed.

Apply pesticides so that they do not endanger humans, livestock, crops, beneficial insects, fish, and wildlife. Do not apply pesticides when there is danger of drift, when honey bees or other pollinating insects are visiting plants, or in ways that may contaminate water or leave illegal residues.

Avoid prolonged inhalation of pesticide sprays or dusts; wear protective clothing and equipment if specified on the container.

If your hands become contaminated with a pesticide, do not eat or drink until you have washed. In case a pesticide is swallowed or gets in the eyes, follow the first-aid treatment given on the label, and get prompt medical attention. If a pesticide is spilled on your skin or clothing, remove clothing immediately and wash skin thoroughly.

Do not clean spray equipment or dump excess spray material near ponds, streams, or wells. Because it is difficult to remove all traces of herbicides from equipment, do not use the same equipment for insecticides or fungicides that you use for herbicides.

Dispose of empty pesticide containers promptly. Have them buried at a sanitary land-fill dump, or crush and bury them in a level, isolated place.

NOTE: Some states have restrictions on the use of certain pesticides. Check your state and local regulations. Also, because registrations of pesticides are under constant review by the Federal Environmental Protection Agency, consult your county agricultural agent or state extension specialist to be sure the intended use is still registered.



Use Pesticides Safely
FOLLOW THE LABEL

U.S. DEPARTMENT OF AGRICULTURE

Heidmann, L. J. 1984. Using herbicides for reforestation in the Southwest. USDA Forest Service General Technical Report RM-103, 11 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Site preparation is essential to successfully regenerate conifer stands in the Southwest. Selection of herbicides used to prepare regeneration sites, calibration of equipment, methods of application, and safety are discussed.

Keywords: Herbicides, site preparation, reforestation, ponderosa pine

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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Flagstaff, Arizona
Fort Collins, Colorado*
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Lincoln, Nebraska
Rapid City, South Dakota
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*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

A Classification of Forest Habitat Types of the Lincoln National Forest, New Mexico

Billy G. Alexander, Jr.
Frank Ronco, Jr.
E. Lee Fitzhugh
John A. Ludwig



General Technical Report RM-104
Rocky Mountain Forest and
Range Experiment Station
Forest Service
U. S. Department of Agriculture

Abstract

Vegetational data were collected from the Lincoln National Forest, New Mexico, to develop a forest habitat classification based on potential natural vegetation. There are 13 habitat types and, in addition, several phases identified on the Lincoln National Forest; 8 were previously classified by Moir and Ludwig (1979), and 5 by this study. The 13 habitat types represent 6 climax forest series: *Abies lasiocarpa*, *Picea engelmannii*, *Picea pungens*, *Abies concolor*, *Pseudotsuga menziesii*, and *Pinus ponderosa*. Each habitat type is described according to vegetational composition, topographical occurrence, soils information (when known), ecotones, adjacent habitat types, and general features.

A Classification of Forest Habitat Types of the Lincoln National Forest, New Mexico¹

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¹*This work was performed under contract with the Rocky Mountain Forest and Range Experiment Station, with central headquarters maintained in Fort Collins, Colo., in cooperation with Colorado State University. Supervision was provided by the Station's Research Work Unit at Flagstaff, Ariz., in cooperation with Northern Arizona University.*

²*The work was conducted as part of the requirement for the Master of Science degree at Northern Arizona University.*

³*The work was conducted while the author was Assistant Professor, Northern Arizona University.*

Contents

	Page
INTRODUCTION	1
STUDY AREA	1
METHODS	4
FIELD SAMPLING	4
DATA ANALYSIS	4
RESULTS AND DISCUSSION	5
SPRUCE-FIR HABITAT TYPES	5
<i>Abies lasiocarpa</i> Series	5
<i>Abies lasiocarpa</i> / <i>Senecio sanguisorboides</i> habitat type	5
<i>Picea engelmannii</i> Series	6
<i>Picea engelmannii</i> / <i>Acer glabrum</i> habitat type	6
<i>Picea engelmannii</i> / <i>Elymus triticoides</i> habitat type	7
MIXED-CONIFER HABITAT TYPES	7
<i>Picea pungens</i> Series	7
<i>Picea pungens</i> / <i>Fragaria ovalis</i> habitat type	7
<i>Abies concolor</i> Series	8
<i>Abies concolor</i> / <i>Acer grandidentatum</i> habitat type	8
<i>Abies concolor</i> / <i>Elymus triticoides</i> habitat type	9
<i>Abies concolor</i> / <i>Acer glabrum</i> habitat type	9
<i>Abies concolor</i> / <i>Quercus gambelii</i> habitat type	10
<i>Abies concolor</i> /Sparse undergrowth habitat type	12
<i>Abies concolor</i> / <i>Juglans major</i> habitat type	12
<i>Pseudotsuga menziesii</i> Series	13
<i>Pseudotsuga menziesii</i> / <i>Quercus gambelii</i> habitat type	13
PONDEROSA PINE HABITAT TYPES	14
<i>Pinus ponderosa</i> Series	14
<i>Pinus ponderosa</i> / <i>Quercus gambelii</i> habitat type	14
<i>Pinus ponderosa</i> / <i>Quercus undulata</i> habitat type	14
SUMMARY AND CONCLUSIONS	15
LITERATURE CITED	16
APPENDIXES	19
A. Keys to the Climax Forest Series and Habitat Types of the Lincoln National Forest	19
B. Plant List of All Species Identified in Study	20
C. Successional Status of Major Tree Species Within Habitat Types	23
D. Average Density and Constancy of Tree Species by Habitat Type and Phase	24
E. Average Cover and Constancy of Major Shrub and Herbaceous Species by Habitat Type and Phase	26

A Classification of Forest Habitat Types of the Lincoln National Forest, New Mexico

Billy G. Alexander, Jr., Frank Ronco, Jr., E. Lee Fitzhugh,
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INTRODUCTION

This vegetational classification of forest habitat types for the Lincoln National Forest is applicable to all climax forest series from the low-elevation ponderosa pine to the high spruce-fir. It is based on the concept of potential natural vegetation. The habitat types described here are believed to represent forests in a mature, nondisturbed condition or climax state.

Site classification is important from a management standpoint because it helps to provide a crucial understanding of the ecological aspects of Southwestern forests. It also provides an organizational step in predicting ecological responses to forest treatments. Forest classification based on potential natural vegetation is relatively new to the Southwest. Previous classification work on the Lincoln National Forest by Moir and Ludwig (1979) identified ten mixed conifer and spruce-fir forest types. Dye and Moir (1977) described the compositional elements of a spruce-fir forest near Sierra Blanca Peak on the Lincoln National Forest. Their study showed possible similarities between the southern and northern spruce-fir forests in the Rocky Mountains. Hanks and Dick-Peddie (1974) studied successional trends in the White Mountains, a prominent range of mountains on the Lincoln, and identified various stages of succession after disturbance. Hanks (1966) presents a somewhat more basic synthesis of a similar nature.

In addition to developing a forest habitat type classification for the Lincoln National Forest, this study also involved three other objectives: (1) to test previous classification work by Moir and Ludwig (1979), (2) to clarify successional trends, and (3) to propose management applications. Although some management implications may be inferred, or explicitly stated, from the habitat type descriptions, full development of this subject must await future studies and summaries of existing information.

Although the terminology used in this paper is commonly accepted and follows that of Daubenmire (1968), who presents a comprehensive discussion of terminology, the following terms are defined for emphasis.

plant association is the dominant plant community presenting *potential natural vegetation*, which is the climax vegetation existing on a site after natural succession has occurred in the absence of disturbance. All the areas that are capable of supporting the same plant association are termed a *habitat type* (HT), while a *phase* (P) is a subdivision of the habitat type based on the presence or abundance of an indicator species.

STUDY AREA

The Lincoln National Forest, located in south-central New Mexico, contains some of the southernmost extensive stands of forest in the western United States. The Forest lies east of the Rio Grande River, west of the Texas High Plains, south of the contiguous Rocky Mountains, and north of the Chihuahuan Desert (fig. 1). It is distinct from the Colorado Plateau, and lies in an area that is heavily faulted. As with many Southwestern mountains, those on the Lincoln National Forest are surrounded by desert or grassland, and can be characterized as biogeographical islands. This isolation has special importance in comparing vegetation characteristics between forests of the Southwest (Shreve 1922), and apparently has led to speciation and endemic ecological types in the southwestern United States.

Geography.—The Lincoln National Forest is divided into fragmented mountain ranges, resulting in a mosaic of isolated forests separated by treeless zones. Furthermore, differences between these fragmented mountains and areas outside the Lincoln National Forest appear to be greater than differences within. Thus, a regional

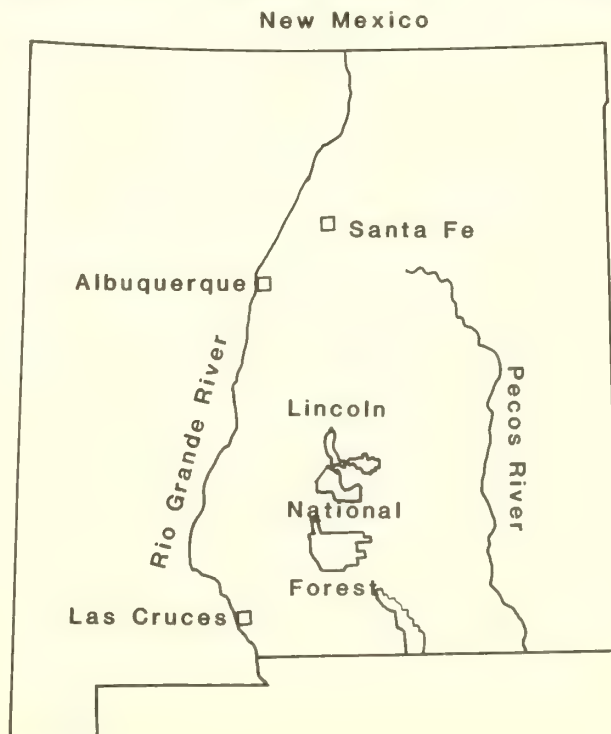


Figure 1.—Location of the Lincoln National Forest in the State of New Mexico.

identity is established for the Forest as far as vegetational habitats are concerned. Four distinct areas are recognized (fig. 2). The Sacramento Mountains are the southern extent of this study, while to the north lie the White Mountains, which include Sierra Blanca Peak. North and east of the White Mountains are a series of smaller mountains—the Carrizo Peak area, including the Jicarrillo and Patos Mountains, and the Capitan Peak area. The Guadalupe Mountains to the south were not included because they did not contain sufficient forested area to meet the objectives of the study.

Geology.—The mountains of the Lincoln National Forest are geologically diverse, with steep elevational relief resulting from numerous uplifts and extrusive actions. The Sacramento Mountains arose primarily from a massive uplift, as evidenced by a steep escarpment on the western flank. The predominant parent material is San Andres Limestone, but in some areas, the underlying Yeso Siltstone is a prominent feature (Weber 1964, Hunt 1977). In addition, the White Mountains, Carrizo Peak area, and the Capitan Mountains are characterized by extrusive volcanic activity and more diverse parent materials. The Sierra Blanca and Nogal Peak areas are dominated by andesitic parent material, and dikes and volcanic plugs often can be found. The Capitan Peak system—a large, linear, east to west range—also exhibits parent material similar to that of the White Mountains. However, the rock has a much redder hue and has been referred to as alaskite.⁴ It appears that the Carrizo Peak area is geologically similar.

⁴Personal communication with Cliff Landers, Soil Scientist, USDA Forest Service, Lincoln National Forest, 1979.

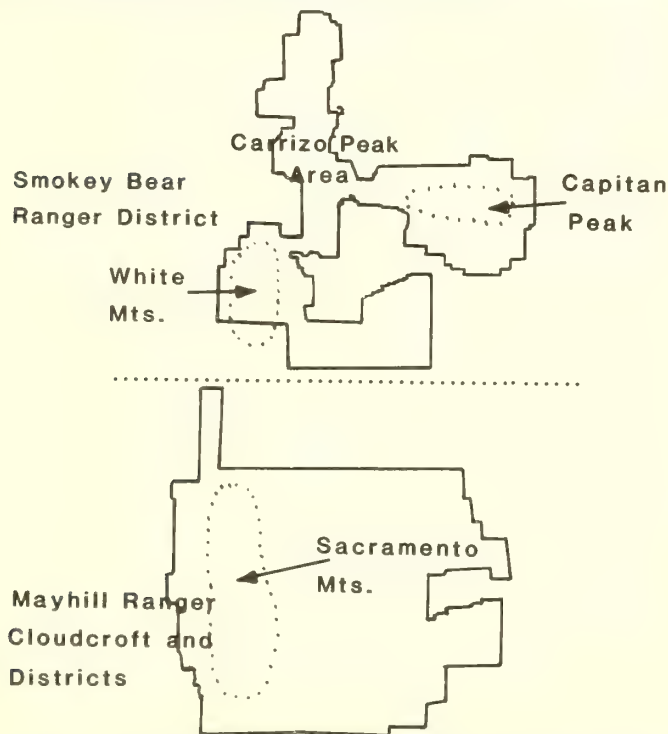


Figure 2.—Geographical divisions of the Lincoln National Forest.

Topography.—Extrusions and uplifts created the typical topographical features of the Lincoln National Forest and probably were largely responsible for the resultant vegetational patterns. The uplifts resulted in steep westerly faces in the Sacramento and White Mountains. In the Sacramento Mountains, the east side exhibits a more gentle overall slope, while the east side of the White Mountains is quite steep as a result of volcanic extrusions.

The steep west and gentle east slope configurations result in narrow vegetational bands on west slopes and wider bands on east slopes. Vegetation on steep slopes exhibits a sharp transition between the xeric pinyon-juniper woodlands and the more mesic mixed conifer stands. The intervening ponderosa pine forest in this area is nearly absent, or at best forms an ecotone. Although other environmental factors undoubtedly exert an influence, the sharp delineation of vegetation, probably results primarily from the behavior of northeasterly-easterly summer storms arising in the Tularosa Basin to the west; as these storms move into the mountains, steep elevational gradients create a dramatic increase in precipitation.

The northern half of the Forest has had more volcanic activity, hence the easterly slopes may be as steep as the west slopes. However, on the west slope of both the White Mountains and Carrizo Peak this sharp vegetational zonation appears once again. The Capitan Mountains exhibit great relief on both the north and south slopes, with long alluvial fan systems at lower elevations. The east slope of Capitan Peak is fairly unique, being quite steep and highly dissected.

The presence of water on the Lincoln National Forest is quite variable. Many perennial streams flow in the Sacramento Mountains, creating wet meadows in valleys, whereas agricultural activities in other valleys have led to draining of meadows. The White Mountains to the north also are bisected by several perennial streams, which are utilized for recreation. In contrast, no perennial streams are present either on Carrizo Peak or Capitan Peak, but many springs and ephemeral streams provide habitats for riparian vegetation.

One of the interesting geological features on the Lincoln National Forest is the presence of rock glaciers in the Capitan Peak area. From the ground, the rock slopes appear to be ordinary scree, but viewed from the air the rock can be seen to have slowly crept down the mountain side. These rock glaciers, while exhibiting sparse vegetational cover, influence water relations on the slope below.

Climate.—Climate throughout the geographical regions of the Southwest exhibits varying patterns, and is undoubtedly a major factor affecting the occurrence of plant associations. Moving easterly through the Southwest, summer precipitation—beginning in July and ending in September—becomes a more prominent part of the annual pattern. Approximately 60% of the annual precipitation falls during this period, but in some area of the Lincoln National Forest, up to 70% of the rainfall comes during summer months. Spring (from mid-April through June) and fall (October and November) are dr

periods. Annual precipitation for forested areas is between 20 and 30 inches (510 and 760 mm) (fig. 3).⁵

Between 12 and 18 inches (300 and 460 mm) of summer precipitation falls over forested areas, usually as a result of convective storms that develop near the mountains. The major source of moisture for these storms is an influx of moist air from the Gulf of Mexico.⁵ While these storms are an important source of moisture during the growing season, especially for herbaceous plants, it is not clear what effect summer moisture has on tree species. Some studies indicate that winter precipitation is the dominant factor for growth and establishment of trees (Fritts 1974).

Precipitation during the winter wet period is mostly snow, which may arise from continental and maritime polar air masses.⁵ These result in frontal systems from the northwest and west. Precipitation during this period is 8 to 12 inches (200 to 300 mm), which saturates soils during the spring thaw.

Historical events.—Interpretation of past events, natural or human caused, is critical to understanding the current vegetational composition on the Lincoln National Forest. Fire was, perhaps, the most important historical factor. Scars indicate that fire once was an active part of the environment, occurring on the average every 7 or 8 years in Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum*)⁶ forests (Weaver 1951). Biswell (1973) estimated a greater frequency,

⁵USDA, Forest Service, Lincoln National Forest, unpublished hydrological report, 1979.

⁶Nomenclature and authority for plant species identified in this study follow that of Lehr (1978) unless otherwise specified.

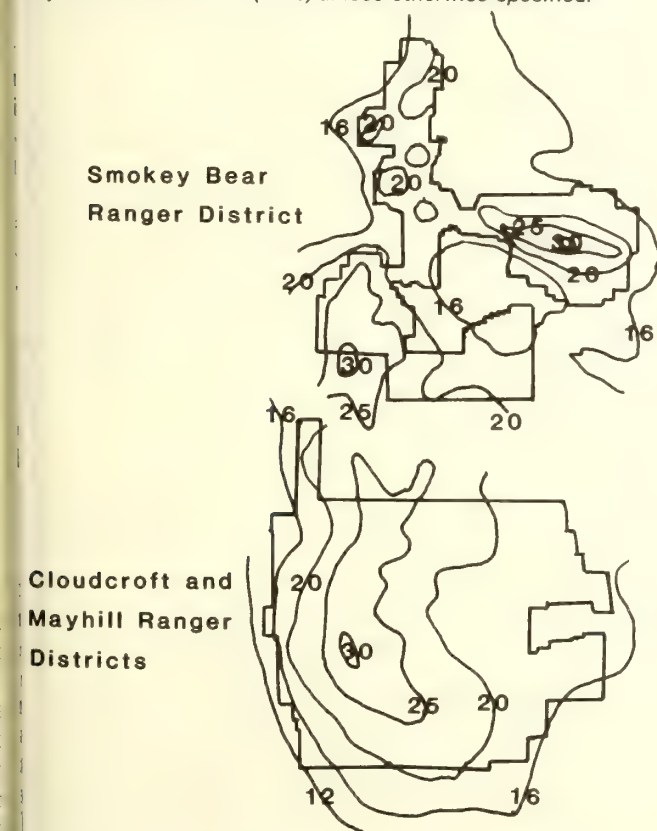


Figure 3.—Annual precipitation for the Lincoln National Forest.

once every 2 or 3 years. The short time span between fires resulted in low-intensity burning conditions of a noncatastrophic nature because of low fuel accumulations. As a consequence, such fire behavior exerted an adaptive pressure on plants comprising the ecosystem.

Ponderosa pine is considered a fire-adapted plant. This adaptation appears to have had a profound effect on Southwestern forests which, if left undisturbed, probably would have reached a climax stage composed of less fire-resistant mixed conifer species. Pine overstories essentially were not damaged by the consumption of light fuels and grassy vegetation. Because of greater resistance of pine reproduction to fire, the species could maintain itself and form relatively pure stands. As a consequence, ponderosa pine stands were maintained in a seral state in what otherwise would be mixed conifer forests.

A similar situation also may have existed in the pinyon-juniper transition zone at lower elevations. Fire excluded the less resistant junipers (*Juniperus* spp.) and pinyon (*Pinus edulis*), maintaining again pure stands of ponderosa pine. Essentially, the adaptability of ponderosa pine enabled it to exist in relatively pure stands over a much wider elevational range than if fire had been excluded.

Fire exclusion following settlement and active forest management resulted in invasion by species that are less fire resistant, so that the forest is now in an advanced successional stage in many areas. These forests consist of a mature ponderosa pine overstory, with younger age classes composed of mixed conifer species, such as Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), southwestern white pine (*Pinus strobiformis*), and white fir (*Abies concolor*). Similarly, juniper (primarily *Juniperus deppeana*) and pinyon increased at lower elevations, suggesting that ponderosa pine is seral in such stands. Thus, the zone occupied by pure ponderosa pine stands has been narrowed to those areas where the climate supports climax ponderosa pine forests. This has led to an expression of the climatic climax boundaries of all species independent of the effects of fire. Further discussions of the effects of fire on Southwestern forests can be found in Weaver (1951), Cooper (1960), and Biswell (1973).

The exclusion of high-frequency, low-intensity fires has altered fire behavior on the Lincoln National Forest. High levels of fuel have accumulated, and seedlings of all timber species have increased in number, resulting in very dense fuel ladders. These changes have increased the susceptibility of forests to catastrophic fires and subsequent devastation of the ecosystem. In contrast, some plants are adapted to catastrophic fires; Gambel oak (*Quercus gambelii*) and wavyleaf oak (*Quercus undulata*) are the most notable on the Lincoln National Forest. Old burned areas are now largely fields of oak brush, which do not regenerate easily to conifer species.

Concurrent with increasing suppression of fire, an extensive railroad logging system was established, reaching into nearly every drainage and operating into the mid-1900's. Early logging practices essentially high-

graded the timber, as illustrated by the existence of large stumps next to mature trees deemed not marketable during early harvest.⁷ In many locations, a lack of harvesting technology left old-growth stands untouched in inaccessible areas. These pockets often are examples of potential natural vegetation. In some instances, the effects of logging operations hastened establishment of Douglas-fir and southwestern white pine on sites previously dominated by ponderosa pine.

The Lincoln National Forest, in common with all forests in the Southwest, has an extensive grazing history. Following Spanish settlement, sheep were the first domestic animals to use the range, but cattle followed shortly, creating additional grazing pressure. During World War II, goats grazed extensively on the Lincoln National Forest. Although the heaviest use was in and below pinyon-juniper woodlands, animals also utilized forested areas, especially canyon bottoms and other areas near water. Today, even with regulated grazing, species abundance and composition may be altered in plant communities.

Of the more recent activities, recreation has heavily impacted the Lincoln National Forest. Increased use in the past 20 years indirectly affected plant communities through a shift in management goals, including creation of the White Mountain Wilderness and other recreation areas. The direct effect of recreation was modification of some riparian sites or cool drainages, primarily because these preferred use areas are easily adapted to camping and picnicking.

METHODS

FIELD SAMPLING

Procedures for sampling stands followed that of Daubenmire and Daubenmire (1968) as modified by Pfister and Arno (1980) and Moir and Ludwig (1983). First, to increase efficiency of plot selection, individuals with knowledge of the area were contacted, historical data were reviewed, and aerial photographs were used. After general areas were selected, actual plot establishment in the field was made subjectively using the following criteria: (1) presence of a mature tree canopy of sufficient age to allow the undergrowth to stabilize; (2) presence of an undergrowth that had recovered from any past disturbance, as determined by the absence of various indicators such as plants or physical signs; and (3) determination that a stand did not represent an ecotone, in that the undergrowth species composition was not a transition between two distinct areas.

Data were collected under three different procedures—reconnaissance, analytical, and validation. The reconnaissance is a relatively rapid procedure, allowing a large number of plots to be measured in a shorter time compared to the analytical procedure, which requires more detailed and time-consuming measurements. As the term implies, the validation procedure utilized plots primarily to document the presence of known habitat types, which, therefore, were purposely undersampled.

⁷Personal communication with Bill Stanborough, USDA Forest Service, Lincoln National Forest, Timber Staff, 1979.

Data collected from these plots were similar to, but less detailed than, those of the other two procedures.

Reconnaissance plots were circular (35.8 feet or 10.9 m radius), covering 4,037 square feet (375 m²). Plant canopy coverage of each undergrowth species was visually estimated to the nearest percent. Trees were recorded in size categories: (1) seedlings—up to 4.5 feet (1.37 m) high, (2) small saplings—4.5 feet (1.37 m) tall to 2 inches (5.1 cm) diameter at breast height (d.b.h.), (3) large saplings/poles—2 to 10 inches (5.1 to 25.4 cm) d.b.h., and (4) mature trees—greater than 10 inches (25.4 cm) d.b.h. In addition, a prism tally was taken to determine basal area.

One analytical plot, 49.2 × 82.0 feet (15 × 25 m), was established for about every ten reconnaissance plots, both types of plots providing essentially the same information. Two transect lines, 16.4 feet (5 m) apart, were located parallel to the long axis; 25 rectangular quadrats (7.9 × 19.7 inches or 20 × 50 cm) were spaced at 3.3-foot (1-m) intervals along each transect. Plant cover estimates were recorded in percentage coverage classes according to Hanks, et al. (1983). The primary function of analytical plots was to provide calibration between visual estimates of reconnaissance and validation plots and the more precise measurements obtained from quadrats in the analytical method. Also, calibration served to narrow differences in estimates of cover values between investigators in the same or different areas so that data would be comparable. To facilitate calibration, a visually estimated reconnaissance plot was always measured first on the site of an analytical plot. Results of the two methods were compared in the field before leaving the site, and any discrepancies were adjusted by further examination of the plot.

Site data recorded for all plots included aspect, slope, elevation, location, landform, and position (ridge, upper slope, midslope, lower slope, bench, and streamside). The soil surface was described according to the percent (totaling 100) of exposed rocks and mineral soil, litter, moss and lichens, and vascular plant basal area. In addition, such general observations as evidence of fire, logging and grazing influence, mistletoe incidence, tree canopy cover, and general stand conditions were recorded.

DATA ANALYSIS

Development of the classification involved primarily ecological judgment, but more formal computer analysis also were applied for additional refinement. Initially plots were subjectively grouped into climax forest series according to the dominant overstory species and reproduction. Six series were recognized on the Lincoln National Forest: *Abies lasiocarpa*, *Picea engelmannii*, *Picea pungens*, *Abies concolor*, *Pseudotsuga menziesii*, and *Pinus ponderosa*.

Within a series, individual plots were grouped according to similarities in species composition. Successive refinement utilized relevé tables—data matrices with coverage values of species in plots (Becking 1957).

Constancy was found to be an important element for determining the reliability of a species as being representative of a given kind of stand. In addition to relevés, an analysis of the total list of species and reference to historical data and abiotic features provided further information needed to clarify groupings. Subsequent data analysis utilized ordination—principal component analysis—to improve objectivity, gain additional insight on the interaction of species, substantiate earlier judgments, or reveal types not previously defined (Moir and Ludwig 1983). The process of iterative group refinement—utilizing subjective and analytical computer procedures—was continued until stands were separated into representative units with relatively consistent site characteristics and similar tree, shrub, forb, and graminoid components. When appropriate, these units, or habitat types, were further categorized by phases—a classification level that retains overstory and undergrowth characteristics of habitat types, but differs uniformly and predictably in minor vegetational and site components.

RESULTS AND DISCUSSION

All known habitat types and phases on the Lincoln National Forest, including those developed by this study and by Moir and Ludwig (1979), are listed in table 1, and a key to their identity is shown in appendix A. Habitat types previously described by Moir and Ludwig that were verified but not sampled during this study, are presented essentially as written by these authors.

Nomenclature for habitat types was derived by incorporating the dominant species into the given name. Where habitat types were similar to those already identified outside the study area, the previously assigned name was accepted to retain compatibility between classifications. Subsequent to publication of the work by Moir and Ludwig (1979), nomenclature of the *Abies concolor* series has been revised. More intensive sampling suggested that *Pseudotsuga menziesii* does not always attain the co-climax position it previously was believed to have reached in stands of the *Abies concolor* forest series. As a consequence, *Pseudotsuga menziesii* has been deleted from the name of several *Abies concolor* habitat types. Habitat types that were identified in Moir and Ludwig (1979) as *Abies concolor*-*Pseudotsuga menziesii* . . . now appear as *Abies concolor* . . . in this publication. Habitat types represented by only a few plots were determined by comparing such plots with those located on the Gila and Cibola National Forests (Fitzhugh et al.⁶).

Each habitat type description begins with a discussion of diagnostic vegetation characterizing that type. Overstory tree species are described in relation to their climax and successional roles within the habitat type, and plant species most consistently present or absent in the habitat type are labeled diagnostic. Other plants that are not as important as diagnostic species, but that offer clues to field identification of the habitat type, also

are discussed. Coverage values reported for a particular species in a habitat type are based on plot averages.

A generalized topographical description is given for each habitat type. However, because environmental factors may be interactive and compensating, a number of topographical locations supporting the same habitat type can exist. There are situations, in contrast, where a habitat type is restricted to a particular topographical situation; for example, the *Abies concolor*/*Acer grandidentatum* habitat type. Also included in the habitat type description is a discussion of adjacent habitats and ecotones. A discussion section concludes the description of the habitat type, providing additional information gathered during the course of the study.

SPRUCE-FIR HABITAT TYPES

Abies lasiocarpa Series

***Abies lasiocarpa*/Senecio sanguisorboides habitat type (ABLA/SESA; subalpine fir/burnet groundsel) (from Moir and Ludwig 1979)**

Vegetation.—The overstory is generally dominated by *Abies lasiocarpa*, but sometimes *Picea engelmannii* is co-dominant. *A. lasiocarpa* has moderate to heavy stocking in young and advanced regeneration classes, usually exceeding that of *P. engelmannii*. *Abies concolor* is absent regardless of size class, and *Pseudotsuga menziesii* at low elevations can be a seral component in the stand.

The shrub layer is dominated by either, or both, *Ribes wolfii* and *R. montigenum*. A rich, well-expressed herbaceous layer is dominated by *Senecio sanguisorboides*. Other common species are *Ligusticum porteri*, *Osmorhiza depauperata*, *Actaea arguta*, *Bromus richardsonii*, *Trisetum montanum*, *Festuca sororia*, *Pseudocymopterus montanus*, and *Erigeron superbus*.

Although there possibly may be two phases in this habitat type, they have not been designated as such because of the overall homogeneity of vegetation and the limited distribution of spruce-fir forests in the Sierra Blanca area (Dye and Moir 1977). A typical phase could be found on most sites, whereas the *Pseudotsuga menziesii* phase (stands containing *P. menziesii*) would be restricted to warmer sites at low elevations. In contrast to the typical phase, the *Pseudotsuga* phase exhibits low coverage values of *Ribes*, and *Populus tremuloides* may form a seral community in some locations. In the more typical situation, *Ribes montigenum* and *R. wolfii* increase in abundance, and especially dominate large fire-created openings; *Pseudotsuga* and often *Populus tremuloides* are absent.

Physical setting.—The habitat type is common to the Sacramento Mountains in the vicinity of Sierra Blanca Peak, and is found on all slopes and aspects above 10,000 feet (3,050 m). Soils have developed mostly from Three Rivers material, intrusive monzonite and granite. Soils are primarily Typic and Pachic Cryoborolls, with coarse-loamy texture and good drainage; profiles are deep and have A1-A3-C mineral horizon sequences. Cob-

⁶E. Lee Fitzhugh, William H. Moir, John A. Ludwig, and Frank Conco, Jr. Forest habitat types of the Apache, Gila, and part of the Cibola National Forests. Manuscript in preparation.

Table 1.—List of habitat types and phases on the Lincoln National Forest

Habitat name	Abbreviation	Number of plots
<i>Abies lasiocarpa</i> series		
<i>Abies lasiocarpa</i> / <i>Senecio sanguisorboides</i> habitat type ¹	ABLA/SESA HT	9
<i>Picea engelmannii</i> series		
<i>Picea engelmannii</i> / <i>Acer glabrum</i> habitat type ¹	PIEN/ACGL HT	2
<i>Picea engelmannii</i> / <i>Elymus triticoides</i> habitat type ¹	PIEN/ELTR HT	4
<i>Picea pungens</i> series		
<i>Picea pungens</i> / <i>Fragaria ovalis</i> habitat type	PIPU/FROV HT	5
<i>Abies concolor</i> series		
<i>Abies concolor</i> / <i>Acer grandidentatum</i> habitat type	ABCO/ACGR HT	
<i>Acer grandidentatum</i> typic phase	ACGR typic P	3
<i>Holodiscus dumosus</i> phase	HODU P	3
<i>Abies concolor</i> / <i>Elymus triticoides</i> habitat type ¹	ABCO/ELTR HT	4
<i>Abies concolor</i> / <i>Acer glabrum</i> habitat type	ABCO/ACGL HT	
<i>Holodiscus dumosus</i> phase ¹	HODU P	17
<i>Abies concolor</i> / <i>Quercus gambelii</i> habitat type	ABCO/QUGA HT	
<i>Quercus gambelii</i> typic phase ¹	QUGA typic P	18
<i>Holodiscus dumosus</i> phase ¹	HODU P	7
<i>Festuca arizonica</i> phase ¹	FEAR P	4
<i>Muhlenbergia virescens</i> phase ¹	MUVI P	1
<i>Muhlenbergia dubia</i> phase	MUDU P	2
<i>Abies concolor</i> /Sparse undergrowth habitat type ¹	ABCO/Sparse HT	1
<i>Abies concolor</i> / <i>Juglans major</i> habitat type	ABCO/JUMA HT	4
<i>Pseudotsuga menziesii</i> series		
<i>Pseudotsuga menziesii</i> / <i>Quercus gambelii</i> habitat type	PSME/QUGA HT	
<i>Quercus gambelii</i> typic phase	QUGA typic P	9
<i>Holodiscus dumosus</i> phase	HODU P	6
<i>Pinus ponderosa</i> series		
<i>Pinus ponderosa</i> / <i>Quercus gambelii</i> habitat type	PIPO/QUGA HT	2
<i>Pinus ponderosa</i> / <i>Quercus undulata</i> habitat type	PIPO/QUUN HT	
<i>Quercus undulata</i> typic phase	QUUN typic P	7
<i>Muhlenbergia dubia</i> phase	MUDU P	8
<i>Muhlenbergia longiligula</i> phase	MULO P	2

¹Previously described by Moir and Ludwig (1979).

bles may be very compact below about 12–18 inches (30–45 cm) (Dye and Moir 1977).

Ecotones and adjacent habitats.—Ecotones occur with alpine tundra along high, windswept ridges (Moir and Smith 1970) and with meadows dominated by *Festuca thurberi* (Moir 1967). At lower elevations, mixed conifer forests consist mostly of the *Abies concolor*/*Acer glabrum* habitat type, *Holodiscus dumosus* phase.

Discussion.—This habitat type is situated in a zone of high precipitation, much of which is in the form of snow, and as a consequence, recreational skiing is extensive. The ABLA/SESA HT also serves as the principal watershed for the towns of Ruidoso and Capitan, N. Mex.

This habitat type exhibits high site quality for *Abies lasiocarpa* var. *arizonica*. Robust, long-lived ecotypes and the tallest known specimens grow here, and some individuals often are older than 275 years. Such longevity may explain the higher density of mature *Abies* in this type than in most other spruce-fir habitat types in Arizona and New Mexico. An examination of the structure of six mature stands indicated that the major

climax species in four stands was *A. lasiocarpa* var. *arizonica*, whereas both *Abies* and *Picea engelmannii* occupied the remaining two stands.

According to Dye and Moir (1977), there is no evidence that the majority of adjoining *Festuca thurberi* meadows are fire-initiated precursors of spruce-fir forests. Rather, they appear to be edaphic climaxes on soil that are more finely textured than forest soils (Moir 1967), and may have originated during warmer postglacial climates as forests retreated upward in elevation and grassland vegetation followed.

Picea engelmannii Series

***Picea engelmannii*/*Acer glabrum* habitat type (PIEN/ACGL; Engelmann spruce/Rocky Mountain maple) (from Moir and Ludwig 1979)**

Disjunct outliers of *Picea engelmannii* are found in the Hubbell and Sacramento Canyons of the Sacramen-

Mountains and in the Chiricahua Mountains of Arizona. While these outliers were assigned to the *Picea engelmannii*/*Acer glabrum* habitat type, they are not sufficiently widespread in occurrence to consider the type of major importance on the Lincoln National Forest. *Pseudotsuga menziesii* is the most important codominant tree, and *Acer glabrum* is usually present in the undergrowth. Herbaceous cover in plots ranged from 5% to 7%, with the most constant species being *Bromus richardsonii*, *Viola canadensis*, *Smilacina stellata*, and *Agrosticum porteri*. The habitat type is of interest primarily because Engelmann spruce is present at low elevations (8,900–9,200 feet or 2,710–2,800 m) at its southernmost limit in North America (Chiricahua Mountains, Arizona, lat. 31°52' N.).

***Picea engelmannii*/*Elymus triticoides* habitat type**
PIEN/ELTR; Engelmann spruce/beardless wild rye)
(from Moir and Ludwig 1979)

This habitat type, also considered minor, is restricted to the Capitan Mountains at uppermost elevations. *Pseudotsuga menziesii* is codominant; *Abies lasiocarpa* varies from absent to codominant. A shrubby undergrowth varying in cover density from 2% to 23% consists of *Acer glabrum*, *Holodiscus dumosus*, *Jamesia americana*, and *Ribes* spp. Soils are very cobbly, and undergrowth vegetation appears to be related to the buildup of soils, commencing from raw talus. On better developed soils, *Elymus triticoides* may cover up to about 9% of the surface.

MIXED CONIFER HABITAT TYPES

Picea pungens Series

***Picea pungens*/*Fragaria ovalis* habitat type**
PIPU/FROV; Colorado blue spruce/wild strawberry)

Vegetation.—*Picea pungens* and *Pseudotsuga menziesii* are codominants in this habitat type (fig. 4), each with a density of between 60 and 80 square feet of basal area per acre (13.8 and 18.4 m²/h). *Abies concolor* is rarely always present, but only as a minor climax species. *Picea engelmannii* may be present in small amounts, while *Pinus strobiformis* and *P. ponderosa* are rare components. *Populus tremuloides* is the major successional species following fire and other major disturbances. The shrub layer is highly variable, with *Holodiscus dumosus* and *Acer glabrum* being the most common, but exhibiting little constancy. Often, the shrub component is absent.

Poa pratensis, *Bromus richardsonii*, and *Trisetum montanum* are the three dominant grasses of this habitat type. Coverage of these species may be higher than 80% of the plot—but the grass component is less consistent than the forb layer. *Fragaria ovalis* and *F. vesca* are consistent species in the undergrowth, which is usually dominated by forbs. Other forbs include



Figure 4.—*Picea pungens*/*Fragaria ovalis* habitat type. Plot 855, Cox Canyon, Lincoln National Forest (8,400 feet or 2,560 m). *Pseudotsuga menziesii* codominant with *Picea pungens*; *Abies concolor* common. *Holodiscus dumosus* and *Acer glabrum* often present; *Poa pratensis* also common.

Cystopteris fragilis, *Galium aspernum*, *Dugaldia hoopesii* (*Helenium hoopesii*), *Iris missouriensis*, *Oxalis alpina*, and *Pseudocymopterus montanus*.

Physical setting.—All plots sampled in this habitat type were found in the Sacramento Mountains. The habitat type is restricted to sideslopes near canyon bottoms, at elevations between 8,000 and 9,000 feet (2,440 and 2,745 m) and always on northern exposures. Soils have well-developed litter and duff layers.

Ecotones and adjacent habitats.—A meadow community dominated by *Poa pratensis* can be found in canyon bottoms directly below the PIPU/FROV HT. It is doubtful, however, that the streamside *Picea pungens*/*Poa pratensis* (PIPU/POPR) habitat type occurs here as suggested by Moir and Ludwig (1979). Extensive reconnaissance subsequent to their study has not revealed the PIPU/POPR HT, except possibly as a very narrow ecotone at the forested edge of the meadows.

Pseudotsuga menziesii increases within the PIPU/FROV HT further upslope from the canyon bottom, and is indicative of the *Picea pungens*-*Pseudotsuga menziesii* habitat type described by Moir and Ludwig (1979) on the Lincoln National Forest. As with the PIPU/POPR HT, however, additional studies reported here and elsewhere in Arizona and New Mexico (Fitzhugh et al.,⁸ Alexander et al.,⁹ DeVelice et al.¹⁰) show that such stands should be considered ecotones and not habitat types. These ecotones lie between the PIPU/FROV HT and the *Abies concolor* series habitat types, commonly the *Abies concolor*/*Acer glabrum* habitat type, *Holodiscus dumosus* phase.

Discussion.—The *Picea pungens* series is highly restricted on the Lincoln National Forest, occurring only in cool, moist canyons at mid-elevations. Because of acces-

⁸Billy G. Alexander, Jr., E. Lee Fitzhugh, John A. Ludwig, and Frank Ronco, Jr. Forest habitat types of the Cibola National Forest, New Mexico. Manuscript in preparation.

¹⁰Robert L. DeVelice, John A. Ludwig, William H. Moir, and Frank Ronco, Jr. A classification of forest habitat types in northern Mexico and southern Colorado. Manuscript in preparation.

sibility, these sites historically have been heavily grazed and subsequently subjected to considerable disturbance. Consequently, sampling this series for climax or near-climax stands was difficult, and only seven plots were sampled between this study and that of Moir and Ludwig (1979). All known *Picea pungens* stands, however, were sampled by the two studies.¹¹

A larger sample from the Gila National Forest established the existence of several *Picea pungens* habitat types that are characterized by an abundant grass cover or a dominant forb layer (Fitzhugh et al.⁸). In the Lincoln National Forest, the PIPU/FROV HT identified in this study is clearly forb-dominated and similar to that described on the Gila National Forest by the above authors. DeVelice et al.¹⁰ recognized shrub- and grass-dominated *Picea pungens* habitat types in northern New Mexico. The Cibola National Forest also has shrub-dominated *Picea pungens* habitat types—*Picea pungens*/*Cornus stolonifera*—as well as those of a grass-dominated nature—*Picea pungens*/*Carex foenea* habitat type (Alexander et al.⁹). The Lincoln National Forest, in contrast, lacks the diversity shown in these other areas.

The *Picea pungens* habitat types and communities on the Lincoln National Forest are heavily impacted by humans. Their restriction to mid-elevation, cool, moist canyons and close proximity to water results in heavy use from recreation and livestock activities. The *Picea pungens* forest also is used extensively by wildlife for feeding and traveling between canyon bottoms and the remainder of the forest. Trees in these canyon bottom communities are sparse, with only an occasional individual *Picea pungens* present. The undergrowth composition reflects the high degree of disturbance, with *Poa pratensis* and other indicator species such as *Erodium cicutarium* and *Artemisia dracunculus* being common.

In the ecotone situated above the PIPU/FROV HT, common plants are *Pseudotsuga menziesii*, *Acer glabrum*, and *Holodiscus dumosus*. These species are representative of both the habitat type and the ecotone, but coverage increases with increasing upslope distance from the canyon bottom. The ecotone, however, is absent or minor when ecological boundaries, such as those delineated by cold air drainages, are abrupt, but may be extensive in areas where the environmental change is gradual.

Abies concolor Series

Abies concolor/*Acer grandidentatum* habitat type (ABCO/ACGR; white fir/big tooth maple)

Vegetation.—*Abies concolor* is the primary timber species in the climax community of this habitat type (fig. 5). *Pseudotsuga menziesii* is late successional, but it can occur in climax stands. In younger stands, it is much more numerous. Furthermore, these young stands have dense *Abies concolor* regeneration. *Pinus strobiformis* is always of minor importance in stands of this habitat



Figure 5.—*Abies concolor*/*Acer grandidentatum* habitat type *Holodiscus dumosus* phase. Plot 839, Baily Canyon, Lincoln National Forest (8,440 feet or 2,570 m). *Pseudotsuga menziesii* a prominent member of overstory; *Abies concolor* dominant. *Acer glabrum* present in tree form. Rod graduated in decimeter segments.

type, but is commonly present. In contrast, other timber species, notably *Pinus ponderosa*, are absent.

The diagnostic tall shrub is *Acer grandidentatum* which is always present in contrast to the usual absence of *Acer glabrum*. If present, *A. glabrum* will be subordinate to *A. grandidentatum*, and may represent an ecotone between the ABCO/ACGR HT and the ABCO/ACGL HT. Stands with a high coverage of *A. grandidentatum*, reaching 60% in some instances, often have relatively low coverage of conifer species. *Quercus gambelii* is always present, but coverage is low.

The number of different forbs comprising the undergrowth of this habitat type is indicative of its cool, moist nature. *Thalictrum fendleri* is most common, followed by *Galium boreale* and *Smilacina stellata*. Of interest is the frequent occurrence of *Habenaria sparsiflora*.

***Acer grandidentatum* (ACGR) typic phase.**—This phase represents the drier component of the habitat type, with *Holodiscus dumosus* absent. *Bromus richardsonii* and *Carex* spp. are common.

***Holodiscus dumosus* (HODU) phase.**—In contrast to the typic phase, the HODU phase is found on wetter sites of the habitat type. It is characterized by the presence of the diagnostic species *Holodiscus dumosus*. *Bromus richardsonii* is the only graminoid found in this phase.

Physical setting.—The ABCO/ACGR HT is always found in canyons or similar cool, moist sites. Elevation varies from 6,500 feet (1,980 m) to more than 8,500 feet (2,590 m), with the *Holodiscus dumosus* phase found above 7,500 feet (2,285 m). This habitat type is generally found on northern aspects, but if conditions are sufficiently mesic, it can be found on western and eastern exposures as well.

Ecotones and adjacent habitats.—At lower elevations, steep canyons can result in abrupt environmental

¹¹Personal communication with Timber Staff personnel, USDA Forest Service, Lincoln National Forest, 1979.

changes. In such situations, the community adjacent to the *Abies concolor*/*Acer grandidentatum* habitat type may be the *Pseudotsuga menziesii*/*Quercus gambelii* habitat type or even the *Pinus ponderosa*/*Quercus gambelii* habitat type. Where slopes are more gradual, the adjacent community often is the mesic *Abies concolor*/*Acer glabrum* habitat type, *Holodiscus dumosus* phase.

Discussion.—The ABCO/ACGR HT, at its representative elevation, is the most mesic habitat type of the *Abies concolor* series. It is a highly restricted type, being confined to the lower portion of slopes rising from canyons. Moir and Ludwig (1979) also defined a canyon stream-side ABCO/ACGR HT in Arizona that appears to reflect virtually the same forest and environmental conditions recognized here.

***Abies concolor*/*Elymus triticoides* habitat type
ABCO/ELTR; white fir/beardless wild rye)
from Moir and Ludwig 1979)**

This habitat type is unique and is limited to the Capitan Mountains where it borders the *Picea engelmannii*/*Elymus triticoides* habitat type. *Abies concolor* and *Pseudotsuga menziesii* dominate. *Pinus strobiformis* usually is abundant but not dominant, and at times will be absent. *Picea engelmannii* is absent, while other timber species are rarely found. Common tall shrubs are *Quercus gambelii* and *Holodiscus dumosus*; *Acer glabrum* is absent. The undergrowth is dominated by grasses. *Elymus triticoides* is very abundant, covering up to 80% of a stand. *Bromus richardsonii* also is common, but not as abundant as *E. triticoides*. The forb undergrowth is minimal; no species is constant. This habitat type is within the group of mixed conifer habitats characterized by grass-dominated undergrowth, such as the *Abies concolor*/*Quercus gambelii* and the *Abies concolor*/*Festuca arizonica* habitat types. Soils are extremely cobbly, and grass cover is interrupted by patches of cobbly talus at the surface.

***Abies concolor*/*Acer glabrum* habitat type (ABCO/ACGL;
white fir/Rocky Mountain maple)**

Vegetation.—*Abies concolor* dominates in stands of this habitat type (fig. 6), if not in the overstory then as regeneration. *Pseudotsuga menziesii* is a successional dominant, and it remains a codominant in climax stands, becoming minor in very old stands. *Pinus strobiformis* is similar to *Pseudotsuga menziesii* in behavior, but will not maintain codominant status in older stands. *Pinus ponderosa* occasionally may be present in this habitat type.

The tall shrub layer is highly diagnostic of this habitat type. *Acer glabrum* is always present, ranging from high to low coverage. In the one phase of the habitat type recognized on the Lincoln National Forest, *Holodiscus dumosus* is always present. *Quercus gambelii* is a common component, but when present, always has low coverage values. *Symphoricarpos oreophilus*, while sometimes present, has little diagnostic value.



Figure 6.—*Abies concolor*/*Acer glabrum* habitat type, *Holodiscus dumosus* phase. Plot 840, Baily Canyon, Lincoln National Forest (8,280 feet or 2,525 m). *Abies concolor* and *Pseudotsuga menziesii* dominate these sites; *Pinus strobiformis* common, *Pinus ponderosa* uncommon. *Acer glabrum* and *Holodiscus dumosus* always present.

The only grass of any abundance is *Bromus richardsonii*, which is a common component of the undergrowth. Predominant forbs include *Galium boreale*, *Stellaria longifolia*, and *Thalictrum fendleri*, which can be sufficiently abundant to cover a large percentage of the site.

***Holodiscus dumosus* (HODU) phase.**—This phase is the only form in which the ABCO/ACGL HT occurs on the Lincoln National Forest, and it is characterized by the presence of *Holodiscus dumosus*.

Physical setting.—The ABCO/ACGL HT, HODU phase is found predominantly on north- and northwest-facing slopes, and possibly on more westerly slopes where sites are wet and cool. Its elevational range is broad—from 8,000 feet (2,440 m) to more than 9,500 feet (2,895 m). Where it lies at lower elevations, sites will be locally wet and cool. Therefore, the type is located along canyon sides and cool drainages, and its presence is most striking in cool drainages where the adjacent community may be much drier. At upper elevations, this habitat type occurs along the tops of ridges and knolls. Soils were derived from alluvial deposits or sideslope colluvial parent materials, and the litter layer usually was well developed.

Ecotones and adjacent habitats.—At upper elevations, this habitat type forms ecotones with spruce-fir types. Where environmental conditions are too dry for optimum development of the type, the resulting ecotone will be shared with the adjacent *Abies concolor*/*Quercus gambelii* habitat type, *Holodiscus dumosus* phase. In contrast, the *Abies concolor*/*Acer grandidentatum* habitat type will be found adjacent to the ABCO/ACGL HT, HODU phase, in cool, wet drainages where conditions are especially moist.

Discussion.—This habitat type and associated phase are found in cool, wet sites, and are well represented on the Lincoln National Forest, especially in the Sacramento Mountains. Moir and Ludwig (1979) also described this habitat type and phase as well as a *Berberis repens* phase found in northern New Mexico and an outlier in the White Mountains of Arizona. Hanks (1966) studied successional relationships in the *Holodiscus dumosus* phase and concluded that fire was the principal factor initiating succession. Because of wet conditions existing in mixed conifer forests, historical fires were infrequent, generally light, and erratic. But localized intense fires probably resulted in a patchy or mosaic stand structure (Jones 1974). Logging and stand deterioration with increasing age, however, also contributed to the irregular structure.

While *Quercus gambelii* and *Robinia neomexicana* follow the herbaceous stage and dominate burned-over areas a few years after fires, other important species such as *Acer glabrum*, *Holodiscus dumosus*, and *Ptelea trifoliata* (*P. angustifolia*) also are found in the shrub stage (Moir and Ludwig 1979). In the late coniferous stage of succession, *Abies concolor*, *Pseudotsuga menziesii*, and *Pinus strobiformis* become established. *Pinus ponderosa*, however, is present only occasionally, apparently becoming established in small openings created by hot fires.

***Abies concolor/Quercus gambelii* habitat type (ABCO/QUGA; white fir/Gambel oak)**

Vegetation.—*Abies concolor* and *Pseudotsuga menziesii* are the principal climax timber species of this habitat type, but as the stand matures, the dominant *P. menziesii* is replaced by the more shade tolerant *Abies concolor*. On drier sites of this habitat type, *Pseudotsuga menziesii* maintains itself in a prominent climax role. *Pinus ponderosa* and *P. strobiformis* are common seral trees, but distribution of the latter is highly variable, being much more prominent on wetter than drier sites. Furthermore, it is often absent from older, near-climax stands. Occasional individual *Pinus edulis* and *Juniperus deppeana* trees also can be found on drier sites, especially on those areas where the habitat type grades directly into pinyon-juniper sites.

Quercus gambelii is the prominent shrub component of this forest type, with coverage values up to 5% or greater. Large clumps of *Quercus gambelii* found on these sites may be due to past disturbances, such as local concentrations of heat in widespread burns, which especially favored oak regeneration. *Robinia neomexicana* also may be abundant on disturbed sites.

Grasses of this habitat type are more diverse than those of the wetter ABCO/ACGL HT, but they may be sparse, or nearly absent, or codominant with *Q. gambelii*, depending on the phase of the habitat type. *Bromus richardsonii*, *Festuca arizonica*, and *Poa fendleriana* are encountered most often; other grasses range from the mesic *Elymus triticoides* to the more xeric *Muhlenbergia virescens* and *M. dubia*. *Carex rossii* also is found frequently. Forbs are highly variable, with *Thalictrum*



Figure 7.—*Abies concolor/Quercus gambelii* habitat type, *Holodiscus dumosus* phase. Plot 837, Cloudcroft Experimental Forest, Lincoln National Forest (8,600 feet or 2,620 m). *Abies concolor* dominant; *Pseudotsuga menziesii* often codominant. *Holodiscus dumosus* and *Quercus gambelii* abundant; forbs with high diversity.

fendleri present on most sites. *Clematis ligusticifolia* is common in the *Holodiscus dumosus* phase of the type.

***Quercus gambelii* (QUGA) typic phase.**—With the exception of *Quercus gambelii* (to which grasses are subordinate), the typic phase of the ABCO/QUGA HT is characterized by a lack of any adequate diagnostic species. However, *Poa fendleriana* increases as the stand nears the climax stage.

***Holodiscus dumosus* (HODU) phase.**—The HODU phase (fig. 7) is characterized by the presence of *Holodiscus dumosus*, which may cover as much as 25% of a given site. *Quercus gambelii* still has a high coverage. *Symphoricarpos oreophilus* and *Clematis ligusticifolia* also are common components of this type.

***Festuca arizonica* (FEAR) phase.**—*Festuca arizonica* is the diagnostic species of this phase, with coverage values up to 20%. *Muhlenbergia montana* and *Poa fendleriana* are common. The FEAR phase lacks forb diversity, but *Erigeron platyphyllus*, *Geranium caespitosum* and *Artemisia ludoviciana* are common. This phase of the habitat type is not widespread on the Lincoln National Forest.

***Muhlenbergia virescens* (MUVI) phase.**—This phase (fig. 8) is delineated by the presence of *Muhlenbergia virescens*, which may have up to 60% cover in some areas according to Moir and Ludwig (1979). In addition Moir and Ludwig indicated that *Stipa pringlei* and *Sitonia hystris* may be common, depending on location. Similarly, *Festuca arizonica*, *Poa fendleriana*, *P. interior* and *Koeleria pyramidata* (*K. cristata*) may be present but in minor amounts. They also indicated that the following forbs occasionally may be important: *Pteridium aquilinum*, *Thermopsis pinetorum*, and *Vicia pulchella*.

Overall acreage of this phase is low, and in addition, its distribution is somewhat limited on the Lincoln National Forest.

Muhlenbergia dubia (MUDU) phase.—Of all the types in the *Abies concolor* series, the MUDU phase of the ABCO/QUGA HT is the most xeric. It is distinguished by the presence of *Muhlenbergia dubia*, and is restricted to cool canyons at low elevations. *Pinus ponderosa* increases in abundance on sites where this phase is found. Topographic sites that favor this phase are common in the Capitan Peak area.

Physical setting.—The habitat type ranges in elevation from 6,500 feet (1,980 m) to more than 9,000 feet (2,745 m) on all aspects and a variety of topographical positions, depending on the phase. The MUDU phase is generally restricted to north to northeast slopes or cool canyon bottoms on north-facing mountain sides and, at 6,500 to 7,000 feet (1,980 to 2,135 m), is the lowest representative of the type.

In contrast, the typic and HODU phases starting at 7,000 feet (2,135 m) are the highest, and may extend to above 9,000 feet (2,745 m). The typic phase may be found on most aspects of upper canyons and ridge tops, whereas the HODU phase is found on north and northwest slopes below 8,000 feet (2,440 m) and on east slopes as well at higher elevations. Typically, the HODU phase occupies canyon slopes and, occasionally, upper ridge slopes.

The MUVI phase occupies an elevational range from 7,000 to 8,500 feet (2,135 to 2,590 m) or more. At higher elevations, sites occupied by the phase are typically south facing, tending towards cooler east aspects as elevation decreases.

The various phases of this habitat type may be related, in part to the wide variation of soil parent

materials, stoniness, and depth. These relationships, however, are not clear at the present time.

Ecotones and adjacent habitats.—According to Moir and Ludwig (1979), the typic phase probably is characterized by moderate regimes of temperature and moisture with respect to the environmental gradient within mixed conifer forests. Under more moist situations, the HODU phase is the most prominent adjacent community, but any of the more mesic habitat types also may occupy a similar position. In turn, the HODU phase is bordered by the more mesic ABCO/ACGL HT (HODU phase), with the ecotone between the two types recognized by a decrease in *Quercus gambelii* and an increase in *Acer glabrum*. Furthermore, many areas occupied by the HODU phase are spatially narrow because of sharp local topographical differences. Under certain instances where site conditions are not limiting, the typic phase may be bordered by the MUVI or MUDU phases of the ABCO/QUGA HT.

As sites occupied by the typic phase gradate toward drier conditions, the existing vegetation is replaced by more xeric associations such as the PSME/QUGA HT or various habitat types of the *Pinus ponderosa* series. It also may be bordered on the drier fringes by the MUDU, MUVI, and FEAR phases of the ABCO/QUGA HT. Under restricted topographical conditions, the MUDU phase can lie adjacent to pinyon-juniper woodlands, and as a consequence, it is the lowest elevational representative of the *Abies concolor* series.

Discussion.—The ABCO/QUGA HT had been described previously by Moir and Ludwig (1979), who recognized the typic and two other phases—*Muhlenbergia virescens* and *Festuca arizonica*. Two additional phases, *Holodiscus dumosus* and *Muhlenbergia dubia*, were defined by this study.

Not only is the ABCO/QUGA HT the most extensive habitat type on the Lincoln National Forest, but its widespread distribution and utilization make it an important type throughout the Southwest. According to Moir and Ludwig (1979), most of the type lies in commercial forests and also within grazing allotments. In addition, deer and other wildlife benefit from oaks and other undergrowth species. Its division into phases reflects shifts in the complex environmental factors to which the plant association responds. The HODU phase lies at the mesic end of the moisture gradient, while the MUVI, FEAR, and MUDU phases represent more xeric conditions for this type. Although the relative dominance between various grasses and oak in different phases of the type is not readily explained, the cause may be related to soil variability, especially in regard to rooting volume and stoniness (Moir and Ludwig 1979).

This habitat type exemplifies low-elevation *Abies concolor* forests, as evidenced by sites on the Lincoln National Forest where *A. concolor* grades into pinyon-juniper woodlands. These areas are occupied by the MUDU phase of the habitat type. The two xeric phases of the habitat type, MUVI and MUDU, are not extensive on the Forest, and as a consequence, data from these areas were limited. Further research is needed to refine and more clearly define these two phases.



Figure 8.—*Abies concolor*/*Quercus gambelii* habitat type, *Muhlenbergia virescens* phase. Plot 821, Mill Canyon, Lincoln National Forest (8,660 feet or 2,640 m). This plot exemplifies the young mixed conifer understory with a *Pinus ponderosa* overstory. *Muhlenbergia virescens* a dominant grass.

***Abies concolor*/Sparse undergrowth habitat type
(ABCO/Sparse; white fir/sparse)**

Vegetation.—This type is characterized by an overstory that may contain *Abies concolor*, *Pseudotsuga menziesii*, *Pinus strobiformis*, and *P. ponderosa*, with a very sparse herbaceous undergrowth—mostly less than 1%, but occasionally to 15% coverage. Moir and Ludwig (1979) observed the *Robinia neomexicana* phase of this habitat type in the southern half of New Mexico, which would include the Lincoln National Forest. Undergrowth species present in the Lincoln, although sporadic, are: *Robinia neomexicana*, *Symphoricarpos oreophilus*, *Salix scouleriana*, and *Quercus gambelii*.

Physical setting.—The ABCO/Sparse HT is common on north to east aspects at elevations of 8,000 to 9,000 feet (2,440 to 2,745 m). It may occur at higher elevations on south- to west-facing aspects. This habitat type is typical of cool, dry sites.

Ecotones and adjacent habitats.—On drier sites, the *Abies concolor*/*Quercus gambelii* or the *Pseudotsuga menziesii*/*Quercus gambelii* habitat types may be present at the ecotone. At cooler, wetter borders of this habitat type, stands of spruce-fir forest are found.

Discussion.—Further work is needed to establish the extent of the *Abies concolor*/Sparse undergrowth habitat type on the Lincoln National Forest. Moir and Ludwig (1979) identified the habitat type on the Forest, but their sample was limited. No new stands of this habitat type were found on the Forest during this study. Whether the *Robinia neomexicana* phase or possibly the *Berberis repens* phase occurs here is difficult to determine because of limited data. Fitzhugh et al.⁸ found the *Robinia neomexicana* phase of the habitat type on the Gila National Forest, while DeVilce et al.¹⁰ recognized the *Berberis repens* phase in northern New Mexico. The geographical distinction between the two phases is consistent with the conclusions of Moir and Ludwig (1979). Site quality in this habitat type may be poor to moderate, according to the latter authors.

***Abies concolor*/*Juglans major* habitat type
(ABCO/JUMA; white-fir/Arizona walnut)**

Vegetation.—*Abies concolor* is the dominant climax timber species of this habitat type (fig. 9). *Populus angustifolia*, while nearly always present, varies in dominance; it is sometimes represented only by one or two trees covering large areas of any given plot. *Acer negundo* will be present, but not as a canopy dominant. *Fraxinus pennsylvanica* also is a stand component, being more strongly represented in younger age classes. Although *Juglans major* is only a minor constituent of the overstory, its presence is diagnostic.

Quercus gambelii is not only a common species in this habitat type, but it is sometimes quite abundant considering the riparian nature of the vegetation. *Vitis arizonica* is a common component of the shrub layer. The density of *Poa pratensis*, the only grass of consequence found in this habitat type, was quite high on



Figure 9.—*Abies concolor*/*Juglans major* habitat type. Plot 845, Three Rivers Canyon, Lincoln National Forest (7,100 feet or 2,165 m). *Abies concolor* the climax timber species; *Populus angustifolia* also prominent in overstory. *Juglans major* common along with *Quercus gambelii* and *Vitis arizonica*.

some plots. Few forbs show any constancy whatsoever, and the only one to be found on all sites is *Thalictrum fendleri*.

Physical setting.—The ABCO/JUMA HT, a streamside canyon type, is found only in riparian areas on stream benches. It is well represented near 7,000 feet (2,135 m elevation, but may occur at lower elevations. Aspect does not seem to be a determinant of location; rather water and shade probably are the controlling factors.

Sample stands of this type were found on soils of alluvial origin. The soils observed were very rocky and sandy with a low organic matter component because of frequent flooding and high stream flows.

Ecotones and adjacent habitats.—The ABCO/JUMA HT is restricted to water courses that traverse many different vegetational zones as elevation changes. As a consequence, a variety of habitat types may be found adjacent to the ABCO/JUMA HT. In lower elevations, the type can border pinyon-juniper woodlands. With increasing elevation, *Pinus ponderosa* and *Pseudotsuga menziesii* habitat types appear beside this riparian type. Finally, as the stream-course sites become even cooler with additional elevational increases, the ABCO/JUMA HT is replaced by other *Abies concolor* habitat types either the ABCO/ACGR HT or the ABCO/ACGL HT. Ecotones involving this habitat type are quite abrupt and narrow because of the corresponding abrupt change in the availability of water over short distances from the stream course.

Discussion.—The ABCO/JUMA HT is a typical riparian habitat type that is quite restricted because adequate water supply is often lacking locally. Furthermore, the sparseness of stream courses on the Lincoln National Forest also limits distribution.

However, the habitat type, when present, provides excellent habitats for wildlife, especially birds, and ma

be a critical habitat component for mammals with daily ranges that extend beyond the boundaries of the type. Snags, particularly *Populus angustifolia*, provide good nesting sites for many species. Because of its association with stream courses and the dense canopy that ameliorates the microclimate, the habitat type is used quite heavily by wildlife seeking water and thermal protection.

Pseudotsuga menziesii Series

Pseudotsuga menziesii/*Quercus gambelii* habitat type (PSME/QUGA; Douglas-fir/Gambel oak)

Vegetation.—*Pseudotsuga menziesii* is the dominant climax tree species of this habitat type (fig. 10), whereas *Abies concolor* is conspicuously absent. *Pseudotsuga menziesii* is much more abundant than in habitat types of the *Abies concolor* series, as evidenced by more regeneration under the canopy. *Pinus strobiformis* can be considered subclimax because it is abundant, although it is more variable than *Pseudotsuga menziesii*. Successionally, *Pinus ponderosa* forms a disclimax in this habitat type because of its adaption to fire. Many climax stands show evidence of old fire-scarred *P. ponderosa* being replaced by *Pseudotsuga menziesii* and *Pinus strobiformis*. No regeneration of *Pinus ponderosa* can be seen in the understory. On many drier sites, *P. ponderosa* may become late successional, bordering on a climax element. Also in drier, low-elevation sites, *Pinus edulis* may be present, primarily in the regeneration age class. However, it probably does not play a role in the *P. ponderosa* disclimax because a fire frequency that limits establishment of *Pseudotsuga menziesii* may have a similar effect on *Pinus edulis*. It also is not found in climax stands represented by this habitat type. In addition to *P. edulis*, *Juniperus deppeana* is occasionally found on drier sites.

***Quercus gambelii* (QUGA) typic phase.**—*Quercus gambelii* is the dominant tall shrub species, with an areal coverage of up to 30% in some plots. A slight increase in diversity of shrubs was noticed at lower elevation sites; especially common were *Cercocarpus montanus* and *Rhus trilobata*. The number of grass species increases in this habitat type over that found in the *Abies concolor* series. *Bromus richardsonii* is a common species, while other species of a sporadic nature include *Poa fendleriana*, *Muhlenbergia pauciflora*, *Sitanion hystrix*, and *Stipa pringlei*. Forbs found in the type are characteristic of more mesic sites; *Chaptalia alsophila* is common, but *Galium boreale*, *Lathyrus arizonicus*, and *Pseudocymopterus montanus* also can be expected in the undergrowth.

***Holodiscus dumosus* (HODU) phase.**—Because of its more mesic character, this phase of the habitat type has fewer *Pinus ponderosa*, especially in older stands. *Pinus edulis* is only accidental, and *Juniperus deppeana* is rare. *Holodiscus dumosus* is diagnostic for delineating the phase, but *Quercus gambelii* is still quite abundant and always intermixed with *Holodiscus dumosus*. Generally, the diversity of grasses decreases in this phase—



Figure 10.—*Pseudotsuga menziesii*/*Quercus gambelii* habitat type, *Holodiscus dumosus* phase. Plot 860, Wet Burnt Canyon, Lincoln National Forest (7,280 feet or 2,220 m). *Abies concolor* absent, *Pseudotsuga menziesii* dominant, *Pinus strobiformis* and *Pinus ponderosa* common particularly on seral sites; *Quercus gambelii* the dominant shrub.

Bromus richardsonii is quite constant, while other species are rare. Forbs increase in both diversity and constancy; *Chaptalia alsophila*, *Cystopteris fragilis*, *Galium boreale*, *Geranium caespitosum*, *Pseudocymopterus montanus*, *Senecio sacramentanus*, *Smilicina* spp., and *Thalictrum fendleri* can be expected in the herbaceous layer.

Physical setting.—Both the QUGA typic and HODU phases can be found on canyon sideslopes and ridgetops at elevations ranging from 7,200 to 8,500 feet (2,195 to 2,590 m). The *Holodiscus dumosus* phase is situated on northwest to northeast aspects, whereas the typic phase is not limited to any particular aspect. In many cases, the organic layer at the mineral soil surface was poorly developed, and sites were rocky.

Ecotones and adjacent habitats.—At higher elevations, the habitat type may occur as a pocket within habitat types of the *Abies concolor* series, while dry south slopes may exhibit the typic phase, which commonly borders *Pinus ponderosa* habitat types at lower elevations. The *Holodiscus dumosus* phase borders *Abies concolor* habitat types and at lower elevations is found on north-facing slopes. Because this single habitat type of the *Pseudotsuga* series borders habitat types of two other distinct series, the transition often is obvious; decreasing densities of *Abies concolor* and *Pinus ponderosa* as climax species at higher and lower elevations, respectively, signify the change in habitat.

Discussion.—Because of increased exclusion of fire, vegetation in the habitat type is approaching a climax state and, as a result of higher stocking densities, competition between climax *Pseudotsuga menziesii* and seral *Pinus ponderosa* most likely has intensified. As a consequence, the productivity of *Pinus ponderosa* prob-

ably is lowered. The increased fire hazard from heavier fuel accumulations has been discussed earlier.

It is noteworthy that the habitat type is absent from certain localities on the Forest. Large areas on the eastern slope of the Sacramento Mountains are covered by this habitat type, but northern flanks of mountains elsewhere on the Lincoln generally do not exhibit such large areas of the PSME/UGA HT. These geographical differences in distribution probably are related to climatic variations attributable to topographical differences.

PONDEROSA PINE HABITAT TYPES

Pinus ponderosa Series

Pinus ponderosa/*Quercus gambelii* habitat type (PIPO/UGA; ponderosa pine/Gambel oak)

Vegetation.—*Pinus ponderosa* is the dominant climax timber species in the PIPO/UGA HT (fig. 11), while all other mixed conifer species are absent, with the exception of the rare occurrence of *Pseudotsuga menziesii* and *Pinus strobiformis*. *Pinus edulis* and *Juniperus deppeana* are common, but are not dominant elements of the overstory.

Quercus gambelii is the only shrub that consistently grows in this habitat type, often forming dense clumps. Prominent grass species include *Poa fendleriana* and *Koeleria pyramidata* (K. *cristata*), with *Poa fendleriana* occurring most consistently. These two species are considered relatively better adapted to mesic conditions compared to grasses of drier *Pinus ponderosa* habitat types. *Artemisia* spp. are usually present, *A. ludoviciana* being common; *Erigeron* spp. and *Lithospermum multiflorum* also are common forbs.

Physical features.—The PIPO/UGA HT is generally found on canyon side slopes or upper ridges of northwest, north, and northeast exposures at elevations near 7,000 feet (2,135 m). Patches of exposed mineral soil often can be found in open areas, along with evidence of surface runoff. Also, accumulation of oak and conifer litter may be high under a closed canopy.

Ecotones and adjacent habitats.—At the lower elevational limits of this habitat type, transition to either the drier *Pinus ponderosa*/*Quercus undulata* habitat type or to pinyon-juniper woodlands occurs. Transitions at upper elevations are usually to the more mesic PSME/UGA or ABCO/UGA habitat types.

Discussion.—This habitat type does not appear to be extensive on the Lincoln National Forest. It may, however, be more widely distributed on the Mescalero Apache Indian Reservation, since larger geographical areas lie within the normal elevational range of the habitat type.

The PIPO/UGA HT is, perhaps, under-sampled in this study, primarily because of disturbance that was particularly evident near Ruidoso, N. Mex. Logging, which was extensive in this area, commonly removed all mature trees and left young stands with few clues as to the climax conditions. Consequently, successional



Figure 11.—*Pinus ponderosa*/*Quercus gambelii* habitat type. Forest 830, Windy Canyon, Lincoln National Forest (6,920 feet or 2,110 m). *Pinus ponderosa* dominant; no mixed conifer species; *Quercus gambelii* abundant.

studies are needed to establish the extent of forest covered by this habitat type, which is similar to several stages of the PSME/UGA HT.

Pinus ponderosa/*Quercus undulata* habitat type (PIPO/QUUN; ponderosa pine/wavyleaf oak)

Vegetation.—*Pinus ponderosa* is the climax dominant tree species in the three phases of this habitat type (fig. 12). *Pinus edulis* and *Juniperus deppeana* are minor climax species, and are more abundant in the *Quercus undulata* phase than the other two phases.



Figure 12.—*Pinus ponderosa*/*Quercus undulata* habitat type. Forest 817, Upper Carr Canyon, Lincoln National Forest (6,960 feet or 2,120 m). *Pinus ponderosa* dominates canopy, with *Juniperus deppeana* and *Pinus edulis* present. *Quercus undulata* very abundant, over 5% of site covered.

Quercus undulata is the diagnostic undergrowth species for the habitat type, being most abundant in the QUUN phase and decreasing to 5% coverage in the others. It readily hybridizes with other species of oak, especially *Quercus gambelii* and *Q. grisea*, making identification difficult. Generally, characteristics of *Quercus undulata* are evident in all oak species in this habitat type.

Muhlenbergia dubia is a consistent component of the grassy vegetation comprising this habitat type. Other grass species commonly found in all phases of the habitat type include *Aristida arizonica*, *Bouteloua curtipendula*, *Lycurus phleoides*, and *Schizachyrium scoparium* (*Andropogon scoparius*). The forb layer is not well developed: however, *Artemisia ludoviciana*, *Erigeron divergens*, and *Lithospermum multiflorum* are common.

***Quercus undulata* (QUUN) typic phase.**—This typic phase of the habitat type can be distinguished by the high oak coverage, ranging between 5% and 15%. *Muhlenbergia dubia* and *M. emersleyi* each have a coverage of about 1%.

***Muhlenbergia dubia* (MUDU) phase.**—The diagnostic species identifying this grassy phase is *Muhlenbergia dubia*, covering 3% to 8% of the ground surface. *Muhlenbergia emersleyi* also is found in this phase, often as abundant as *M. dubia*.

Lower coverage values for *Quercus undulata* (less than 5%) and resultant higher coverage values for *M. dubia* (greater than 1%) help to distinguish this phase from the QUUN phase.

***Muhlenbergia longiligula* (MULO) phase.**—This phase is characterized by the dominance of *M. longiligula*, although *M. dubia* will occasionally be present. *Piptochaetium fimbriatum* and *Bouteloua gracilis* also are abundant components of this phase.

Physical features.—The PIPO/QUUN HT occupies nearly all topographical situations and all aspects, most commonly south to southeasterly. It is found between 5,500 and 8,000 feet (1,980 and 2,440 m). As in the PIPO/QUGA HT, exposed mineral soil and evidence of surface runoff can be observed, but usually there is a well-developed litter layer from high coverage of oaks and grasses.

Ecotones and adjacent habitats.—The PIPO/QUUN HT is the driest habitat type of the *Pinus ponderosa* series. The QUUN phase of this habitat type borders pinyon-juniper woodlands. The MUDU phase of the habitat type adjoins either the QUUN phase or gradates directly into pinyon-juniper types on the Lincoln National Forest (Kennedy 1983). Within the Sacramento Mountains, the spatial transition from the MUDU phase into the QUUN phase can be gradual as *Quercus undulata* slowly increases in abundance. The MULO phase of this habitat type tends to be found in islands within areas covered by the MUDU phase. The upper elevational limits of the PIPO/QUUN HT are bordered by either the PIPO/QUGA HT or the PSME/QUGA HT, depending on the abruptness of the transition to wetter, cooler conditions.

Discussion.—The PIPO/QUUN HT, while not extensive, is distributed throughout the Lincoln National Forest. It is, however, restricted to rather narrow elevational belts lying between the pinyon-juniper and mixed conifer forests. Historically, fire probably was an important element in the successional development of this habitat type, observational evidence suggesting that such fires burned with high intensities but low frequencies.

Of interest is the diversity of this type on the eastern flank of Capitan Peak. Chinquapin oak, *Quercus muehlenbergii*, may appear on canyon soils where this type occurs. On canyon sideslopes, much more pinyon-juniper is found mixed with *Pinus ponderosa*.

SUMMARY AND CONCLUSIONS

There are 13 forest habitat types on the Lincoln National Forest. Types range from the cold *Picea engelmannii* series through the warm *Pinus ponderosa* series. This study partitioned forest diversity into recognizable taxonomic units. The ultimate objective of providing land managers with predictive capabilities can be realized only by refinement of the classification and by correlating management implications with habitat types. The refining process may be accomplished best by successional studies, which will identify the seral stages in the ecosystem preceding the climax stage. Similarly, synthesis of existing information and additional research are needed to more fully understand the response of habitat types to natural and human-related activities.

The *Picea engelmannii* and *Abies lasiocarpa* series are found at high elevations in the Sacramento Mountains, White Mountains, and Capitan Mountains. These series represent the coldest and snowiest forested types of the southwestern United States. However, the description of these high-elevation spruce-fir habitat types differs from related types in the northern parts of the Rocky Mountains (Daubenmire 1943, 1952; Oosting and Reed 1952; Ellison 1954; Langenheim 1962; Pfister et al. 1977; Steele et al. 1981). These differences probably result from the combined effect of isolation and lack of genetic exchange between forests of southern New Mexico and other areas.

The *Picea pungens* series is a very restricted group of habitat types, and is not an extensive timber producer in the Southwest or on the Lincoln National Forest in particular. Habitat types of this series are indicative of cool, moist canyons at mid-elevations. These attractive sites have historically been exploited, and few stands remain that exhibit even remnants of pristine conditions.

The most extensive series on the Lincoln National Forest is *Abies concolor*, which exhibits a great diversity of habitat types because of its wide amplitude. Timber species within the series include the lower valued *Abies* and other softwoods of higher value—*Pseudotsuga menziesii*, *Pinus strobiformis*, and *P. ponderosa*. Site conditions in the series range from mesic habitat types where dominance by *Abies* is expressed in early successional

stages, to the drier types in which the more valuable species dominate the seral stages, although *Abies* ultimately occupies the climax position.

An interesting question is posed by the *Pseudotsuga menziesii* series: Is it a climatic climax, an edaphic climax, or are pure stands of *P. menziesii* a result of a lack of an *Abies concolor* seed source? Furthermore, *Pseudotsuga* stands must be critically evaluated to determine if the type is maintained by disturbance to the exclusion of *Abies*, or if it is truly a response to climatic or edaphic conditions. The lack of a seed source apparently can be ruled out because, in this study, stands lacking *A. concolor* were found adjacent to *P. menziesii* stands in which *A. concolor* reproduction was abundant. While no disturbance was observed in these *P. menziesii* stands to account for the absence of *A. concolor*, sites probably exist where disturbance is the contributing factor. Disturbance most often is caused by low-intensity fires and biotic agents such as mistletoe which, by opening the canopy, expose the site to the inhibiting effects of intense solar radiation on the establishment of shade-tolerant species such as *A. concolor* (Ronco 1970, Jones 1974).

The *Pinus ponderosa* series on the Lincoln National Forest has high commercial value, but it is relatively small in size, occupying the area between pinyon-juniper woodlands and mixed conifer forests. Quite often it is absent or occupies a narrow transition zone between the two cover types. Prior to exclusion of low-intensity fires, disclimax *P. ponderosa* types extended into the ecotones of other forest series at lower and higher elevations. Stands in the *P. ponderosa* series often were highly disturbed from catastrophic fires as a result of increased fuels accumulated since fire control measures were initiated. Consequently, locating stands in which to sample was difficult in the present study. Grazing also has commonly contributed to the general disturbance in this series, particularly in the Sacramento Mountains where it has completely altered the species composition in many instances. Because of such widespread disturbance, use of this classification and appropriate keys may be difficult.

Disturbance has had, and probably will continue to have, a major ecological impact on the Lincoln National Forest. Prior to European settlement, fire was the major disturbance, and as a natural part of the ecosystem, exerted adaptive pressures on species inhabiting the ecosystem. This adaptability is most evident in *Pinus ponderosa* forests. In sampling these forests during this study, it became apparent that pure, or nearly pure, stands of *P. ponderosa* once occupied a larger area than they do today, as evidenced by the mature overstory of *P. ponderosa* being replaced by more tolerant mixed conifer species such as *Pseudotsuga menziesii* and *Abies concolor*. Given the assumption that *Pinus ponderosa* is less susceptible to fire than some of the other mixed conifer species, the conclusion can be drawn that these stands were once a *P. ponderosa* disclimax. In order to address these obvious successional changes, land managers must be aware of their existence and adopt fire management policies and silvicultural systems to

favor—depending on management objectives—one or more species having different degrees of fire and shade tolerances.

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APPENDIXES

Appendix A. Keys to the Climax Forest Series and Habitat Types of the Lincoln National Forest

Keys for series and habitat types on the Lincoln National Forest are presented in this section. The first step in using keys in habitat type classification is to determine the series level of a particular site through identification of climax overstory tree species. A climax species is well represented in the overstory of mature stands, and also is reproducing in the understory. In contrast, younger stands will have reproduction of the climax species under the canopy, even though older individuals of the species may not be present in the overstory. Field investigators must judge whether such reproduction will grow to maturity to become the climax dominant when the stand matures. This determination becomes more difficult the younger the stand, especially in the *Abies concolor* series. Similarly, the *Pinus ponderosa* series also will present problems in that reproduction may be sparse on drier sites, forcing investigators to search carefully for *P. ponderosa* reproduction in the ponderosa pine/pinyon-juniper ecotone.

Furthermore, diagnostic species may not always be present in a particular stand because of the lack of a seed source or disturbance. In such instances, the investigator must compare the site in question to written descriptions in order to correctly identify the habitat type. Similarly, when choices in the keys are not clear because of site conditions, written descriptions and synoptic tables should be used to distinguish between types.

A1. Key to Climax Forest Series

1. PIEN or ABLA present in overstory, or regeneration sufficient to confirm their status as climax dominants; PIPU rare, usually absent — 2
2. PIEN and ABLA absent, or if present, then PIPU also prominent — 3
2. ABLA present in overstory and/or as reproduction — ABLA series
2. ABLA absent or accidental — PIEN series
1. PIPU present in overstory and/or as reproduction — PIPU series
1. PIPU absent; ABCO, PSME, or PIPO present — 4
4. ABCO present in overstory, or prominent in understory. ABCO not accidental, truly climax. Other species present but not as climax dominants — ABCO series
4. ABCO absent or accidental, not a dominant component of the overstory or understory — 5
5. PSME clearly the dominant climax species; PIPO late successional; ABCO absent or accidental — PSME series
5. PSME not a strong element of either overstory or understory. PIPO the climax dominant — PIPO series

A2. Key to *Picea engelmannii*, *Abies lasiocarpa*, and *Picea pungens* Series Habitat Types

1. PIPU present in overstory and/or as reproduction — PIPU/FROV HT
1. PIPU absent or accidental — 2
2. ABLA present in overstory and/or as reproduction — ABLA/SESA HT
2. ABLA absent or accidental — 3
3. Low elevation forests, Sacramento Mountains; *Acer glabrum* present — PIEN/ACGL HT
3. High elevation forests, Capitan Peak; *Elymus triticoides* present — PIEN/ELTR HT

A3. Key to *Abies concolor* Series Habitat Types

1. *Acer grandidentatum* present and dominant in association with *A. glabrum* — ABCO/ACGR HT
 - 1a. *Holodiscus dumosus* absent — ACGR typic phase
 - 1b. *Holodiscus dumosus* present — HODU phase
1. *Acer grandidentatum* absent, or not dominant in association with *A. glabrum* — 2
2. Capitan Mountain sites, *Elymus triticoides* abundant — ABCO/ELTR HT
2. Other locations, *Elymus triticoides* rare — 3
3. *Acer glabrum* substantial shrub component, *Pinus ponderosa* absent or accidental — ABCO/ACGL HT
 - 3a. *Holodiscus dumosus* present — HODU phase
3. *Acer glabrum* absent; *Holodiscus dumosus* may be present, but not associated with *A. glabrum*; *Pinus ponderosa* common — 4
4. Riparian sites. *Juglans major* present, *Populus angustifolia* sometimes present — ABCO/JUMA HT
4. Non-riparian sites. *Juglans major* and *Populus angustifolia* absent — 5
5. Understory extremely sparse over wide areas (not isolated pockets). Virtually no shrub representation; grass cover under 2%, diversity extremely low — ABCO/Sparse HT
5. Understory well represented. Shrubs a definite component; *Quercus gambelii* prominent (5% or greater coverage); grasses well represented — ABCO/QUGA HT
 - 5a. *Holodiscus dumosus*, *Festuca arizonica*, *Muhlenbergia virescens*, and *M. dubia* absent — QUGA typic phase
 - 5b. *Holodiscus dumosus* present — HODU phase
 - 5c. *Festuca arizonica* dominant — FEAR phase
 - 5d. *Muhlenbergia virescens* dominant — MUVI phase
 - 5e. *Muhlenbergia dubia* dominant — MUDU phase

A4. Key to *Pseudotsuga menziesii* Habitat Types

1. *Quercus gambelii* the dominant tall shrub ————— PSME/QUGA HT
 - 1a. *Holodiscus dumosus* absent; grass diversity high ————— QUGA typic phase
 - 1b. *Holodiscus dumosus* present; grass diversity low, *Bromus richardsonii* common ————— HODU phase

A5. Key to *Pinus ponderosa* Habitat Types

1. *Quercus gambelii* the prominent oak, no evidence of hybridization with *Q. undulata*. — PIPO/QUGA HT

1. *Quercus gambelii* not the prominent oak, absent or clearly hybridizes with *Quercus undulata*, the dominant oak ————— PIPO/QUUN HT
 - 1a. *Quercus undulata* greater than 5% cover. *Muhlenbergia dubia* usually less than 5% cover ————— QUUN typic phase
 - 1b. *Quercus undulata* with less than 5% cover. *Muhlenbergia dubia* with higher coverages ————— MUDU phase
 - 1c. *Muhlenbergia longiligula* present ————— MULO phase

Appendix B. Plant List of All Species Identified in Study¹

Trees

Abies concolor
Abies lasiocarpa
Acer negundo
Fraxinus pennsylvanica
Juglans major
Juniperus deppeana
Juniperus monosperma
Juniperus osteosperma
Juniperus scopulorum
Picea pungens
Picea engelmannii
Pinus edulis
Pinus ponderosa
Pinus strobiformis
Populus angustifolia
Populus tremuloides
Pseudotsuga menziesii

Shrubs

Acer glabrum
Acer grandidentatum
Berberis fremontii
Berberis repens
Ceanothus fendleri
Cercocarpus montanus
Cornus stolonifera
Fallugia paradoxa
Fendlera rupicola
Gutierrezia sarothrae
Holodiscus dumosus
Jamesia americana
Lonicera involucrata
Parthenocissus inserta
Physocarpus monogynus
Prunus virginiana
Ptelea trifoliata
 (*P. angustifolia*)
Quercus gambelii
Quercus grisea
Quercus muehlenbergii
Quercus undulata
Quercus X (hybrid)
Rhamnus betulaeifolia

Shrubs—continued

Rhamnus californica
Rhus radicans
Rhus trilobata
Ribes spp.
Ribes cereum
Ribes inerme
Ribes montigenum
Ribes pinetorum
Ribes wolfii
Robinia neomexicana
Rosa spp.
Rosa arizonica
Rubus parviflorus
Rubus strigosus
Salix scouleriana
Sambucus glauca
Sambucus microbotrys
Symphoricarpos oreophilus
Vitis arizonica
Yucca angustissima
Yucca baccata

Graminoids

Agropyron trachycaulum
Andropogon gerardi
Andropogon pseudorepens
Aristida arizonica
Blepharoneuron tricholepis
Bouteloua curtipendula
Bouteloua gracilis
Bromus spp.
Bromus marginatus
Bromus richardsonii
Carex spp.
Carex foenea
Carex occidentalis
Carex rossii
Carex siccata
Cyperus fendlerianus
Dactylis glomerata

¹Nomenclature and authority (not shown) follow that of Le (1978).

Graminoids—continued

lymus ambiguus
lymus glaucus
lymus triticoides
estuca arizonica
estuca sororia
estuca thurberi
uncus balticus
Coeleria pyramidata
 (K. *cristata*)
uzula parviflora
ycurus phleoides
Melica porteri
Muhlenbergia dubia
Muhlenbergia emersleyi
Muhlenbergia longiligula
Muhlenbergia montana
Muhlenbergia pauciflora
Muhlenbergia virescens
anicum bulbosum
iptochaetium fimbriatum
oa annua
oa fendleriana
oa interior
oa leptocoma
oa occidentalis
oa palustris
oa pratensis
chizachyrium cirratum
chizachyrium scoparium
 (*Andropogon scoparius*)
itanion hystrix
tipa spp.
tipa columbiana
tipa lettermanii
tipa pringlei
risetum montanum

Forbs

chillea millefolium
 (A. *lanulosa*)
ctaea arguta
goseris glauca
llium spp.
llium cernuum
ndrosace occidentalis
ntennaria parvifolia
quilegia elegantula
rabis fendleri
renaria spp.
renaria lanuginosa
rtemisia carruthii
rtemisia dracunculus
rtemisia frigida
rtemisia ludoviciana
stragalas spp.
stragalus rusbyi

Forbs—continued

Bahia dissecta
Bidens bipinnata
Brickellia californica
Brickellia grandiflora
Calliandra humilis
Campanula rotundifolia
Castilleja spp.
Chaptalia alsophila
Chenopodium album
Chimaphila umbellata
Cirsium parryi
Clematis ligusticifolia
Clematis pseudoalpina
Commelina dianthifolia
Corallorhiza maculata
Corallorhiza wisteriana
Cystopteris fragilis
Delphinium spp.
Draba aurea
Draba helleriana
Dugaldia hoopesii
 (*Helenium hoopesii*)
Epilobium angustifolium
Erigeron divergens
Erigeron flagellaris
Erigeron macranthus
Erigeron platyphyllus
Erigeron superbus
Eriogonum spp.
Eriogonum jamesii
Erodium cicutarium
Erysimum capitatum
Eupatorium herbaceum
Euphorbia fendleri
Euphorbia lurida
Euphorbia palmeri
Fragaria bracteata
Fragaria ovalis
Galium spp.
Galium aspernum
Galium boreale
Galium microphyllum
Galium triflorum
Galium wrightii
Geranium caespitosum
Geranium richardsonii
Goodyera oblongifolia
Habenaria sparsiflora
Haplopappus parryi
Hedeoma drummondii
Hedeoma oblongifolium
Heterotheca fulcrata
Heuchera parvifolia
Hieracium fendleri
Hymenoxys richardsonii
Ipomopsis aggregata
Iris missouriensis

Appendix B—continued

Forbs—continued

Lappula redowskii
Lathyrus arizonicus
Lathyrus eucosmus
Lathyrus leucanthus
Lesquerella gordonii
Ligusticum porteri
Lithospermum multiflorum
Lonicera spp.
Lonicera arizonica
Lonicera utahensis
Lupinus spp.
Lupinus argenteus
Lupinus kingii
Malaxis soulei
Melilotus officinalis
Mirabilis oxybaphoides
Monotropa hypopitys
Myosotis scorpioides
Oenothera hookeri
Opuntia spp.
Orobanche cooperi
Orobanche multiflora
Osmorhiza chilensis
Osmorhiza depauperata
Oxalis alpina
Oxytropis lambertii
Pachystima myrsinites
Pellaea atropurpurea
Penstemon spp.
Penstemon virgatus
Phacelia magellanica
Phlox spp.
Phlox nana
Polygala alba
Polygonum spp.
Potentilla spp.
Potentilla crinita
Potentilla thurberi
Polemonium delicatum
Polemonium foliosissimum
Pseudocymopterus montanus
Psoralea tenuiflora

Pteridium aquilinum
Pyrola secunda
Ranunculus inamoenus
Rudbeckia laciniata
Senecio spp.
Senecio actinella
Senecio arizonicus
Senecio bigelovii
Senecio cardamine
Senecio eremophilus
Senecio hartianus
Senecio lemmoni
Senecio multilobatus
Senecio neomexicanus
Senecio sacramentanus
Senecio sanguisorboides
Senecio spartioides
Senecio wootonii
Silene laciniata
Silene scouleri
Sisymbrium spp.
Sisymbrium altissimum
Smilacina racemosa
Smilacina stellata
Solidago spp.
Stellaria jamesiana
Stellaria longifolia
Swertia radiata
Taraxacum laevigatum
Taraxacum officinale
Thalictrum fendleri
Thermopsis pinetorum
Thlaspi montanum
Townsendia exscapa
Trifolium dubium
Urtica serra
Valeriana spp.
Valeriana capitata
Valeriana edulis
Verbascum thapsus
Vicia spp.
Vicia americana
Vicia pulchella
Viola spp.
Viola canadensis

Appendix C. Successional Status of Major Tree Species Within Habitat Types

C = major climax species S = major seral species a = accidental

c = minor climax species s = minor seral species

Habitat type	Phase	Species										
		ABLA	PIEN	PIPU	POTR	ABCO	PSME	PIST	PIPO	QUGA	PIED	JUDE
ABLA/SESA ¹		C	C	.	S	.	s
PIEN/ACGL ¹		c	C	.	S	.	c
PIEN/ELTR ¹		c	C	.	S	a	c
PIPU/FROV		.	c	C	s	c	C	S	S	.	.	.
ABCO/ACGR	ACGR typic ¹	C	c	c	a	s	.	.
	HODU	C	c	c	a	s	.	.
ABCO/ELTR ¹		.	a	.	.	C	c	c	a	c	.	.
ABCO/ACGL ¹	HODU	C	C	s	a	s	.	.
ABCO/QUGA	QUGA typic ¹	C	C	S	S	S	a	.
	HODU ¹	C	C	c	s	S	.	.
	FEAR ¹	C	C	c	c	S	.	.
	MUVI ¹	C	C	c	S	S	a	.
	MUDU	C	C	c	s	S	a	a
ABCO/Sparse ¹		.	.	.	s	C	C	S	S	.	.	.
ABCO/JUMA		.	.	.	s	C	S	a	S	s	a	a
PSME/QUGA	QUGA typic	C	c	S	S	s	s
	HODU	C	c	S	S	s	a
PIPO/QUGA		C	S	c	s
PIPO/QUUN	QUUN typic	C	s	c	c
	MUDU	C	s	c	c
	MULO	C	s	c	c

¹From Moir and Ludwig (1979).

Species and Size class	ABLA/SESA	PIEN/ACGL	PIEN/ELTR	PIPU/FROV	ABCO/QUGA HT				
	HT	HT	HT	HT	QUGA typic P	HODU P	FEAR P	MUVI P	MUDU P
	(N = 9)	(N = 2)	(N = 4)	(N = 5)	(N = 18)	(N = 7)	(N = 4)	(N = 1)	(N = 2)
<i>Abies lasiocarpa</i>									
Yng regen	99/100	.	3/25
Adv regen	13/100	.	6/50
Mature	12/100	.	1/50
<i>Picea engelmannii</i>									
Yng regen	24/89	16/100	35/100	2/20
Adv regen	9/89	21/100	16/100	2/40
Mature	4/67	10/100	6/100	2/40
<i>Picea pungens</i>									
Yng regen	.	.	.	3/60
Adv regen	.	.	.	3/80
Mature	.	.	.	4/100
<i>Populus tremuloides</i>									
Yng regen	.	.	3/25	.	.	7/14	.	.	.
Adv regen	.	.	1/25	.	3/11	1/14	.	.	.
Mature	7/50	1/11	2/50	2/40
<i>Abies concolor</i>									
Yng regen	.	.	.	9/80	15/83	14/100	6/50	11/100	3/100
Adv regen	.	1/50	.	4/80	8/88	11/100	1/50	13/100	6/100
Mature	.	1/50	.	2/80	3/83	4/86	.	.	1/50
<i>Pseudotsuga menziesii</i>									
Yng regen	.	.	3/50	7/60	19/100	25/100	22/50	8/100	17/100
Adv regen	.	5/100	1/25	11/80	10/88	7/100	3/75	10/100	13/100
Mature	1/22	3/100	9/100	2/100	4/77	1/29	1/50	.	2/50
<i>Pinus strobitiformis</i>									
Yng regen	.	1/50	4/25	3/20	6/72	13/100	15/100	11/100	9/50
Adv regen	.	.	2/50	3/60	10/50	8/86	10/100	6/100	8/50
Mature	.	.	2/50	.	3/27	1/29	1/25	.	4/50
<i>Pinus ponderosa</i>									
Yng regen	.	.	.	1/20	5/38	1/43	5/75	8/100	4/100
Adv regen	8/55	1/29	3/75	39/100	8/100
Mature	.	.	.	1/20	4/61	1/29	5/75	7/100	7/50
<i>Pinus edulis</i>									
Yng regen	2/27	1/14	.	.	.
Adv regen
Mature
<i>Juniperus deppeana</i>									
Yng regen	1/22
Adv regen	2/5
Mature

¹Occurrence of each species in each habitat type and phase is indicated by two values separated by a slash. The first indicates the mean density (in percent) per plot for the tree species. In all cases, however, the first value is the mean for only the plots in which the species was present. The value to the right of the slash is the constancy for each species in the habitat type or phase; it is the percentage of the total number of plots in the group in which the species was found. A dot indicates that the species was not found in a group.

Tree Species by Habitat Type and Phase¹

ABCO/ACGR HT		ABCO/ELTR	ABCO/ACGL	ABCO/Sparse	ABCO/JUMA	PSME/QUGA HT		PIPO/QUGA	PIPO/QUUN HT		
ACGR typic P (N = 3)	HODU P (N = 3)	HT (N = 4)	HT, HODU P (N = 17)	HT (N = 1)	HT (N = 4)	QUGA typic P (N = 9)	HODU P (N = 6)	HT (N = 2)	QUUN typic P (N = 7)	MUDU P (N = 8)	MULO P (N = 2)
.
.	.	.	6/1
.
.
.
.
.
.
.
.	.	.	2/23
.	1/33	3/50	4/29
.	1/33	.	1/6
9/100	46/100	21/100	12/76	100/100	12/75	.	1/17	.	1/14	.	.
14/100	9/100	5/100	10/100	17/100	4/75	.	.	.	1/14	1/25	.
1/67	2/67	2/75	7/88	4/100	5/75	1/13	.
6/100	7/100	25/100	7/94	17/100	1/25	24/100	15/100	.	1/57	3/38	.
6/67	4/100	5/100	5/82	2/100	.	8/100	15/100	.	2/57	2/50	.
.	3/100	3/75	4/76	8/100	1/25	3/89	2/83	.	1/29	1/13	.
5/100	2/67	6/75	2/65	13/100	.	11/89	16/100	.	.	2/13	.
1/67	1/33	8/75	1/47	8/100	.	6/89	9/100	.	.	1/13	.
1/33	2/67	1/25	1/24	.	.	1/44	3/83	.	.	1/13	.
5/100	.	1/25	1/6	.	9/50	5/67	1/17	2/100	12/86	19/100	2/50
7/67	4/75	10/89	3/67	12/50	9/100	28/100	24/100
2/67	1/50	2/67	1/50	2/50	5/100	1/50	6/100
2/33	8/50	19/67	3/50	28/100	18/86	11/100	7/100
1/33	1/33	.	10/100	4/86	4/63	3/50
.
.	3/50	1/33	1/17	2/50	6/86	24/100	7/100
.	1/50	.	1/17	2/50	5/86	7/100	7/100
1/33	1/25	1/11	.	.	1/57	1/63	.

Species and Size class	ABLA/SESA	PIEN/ACGL	PIEN/ELTR	PIPU/FROV	ABCO/QUGA HT				
	HT (N = 9)	HT (N = 2)	HT (N = 4)	HT (N = 5)	QUGA typic P (N = 18)	HODU P (N = 7)	FEAR P (N = 4)	MUVI P (N = 1)	MUDU P (N = 2)
Shrubs									
<i>Acer glabrum</i>	T/33	T/50	2/50	20/60	T/5
<i>Acer grandidentatum</i>	T/5	1/29	.	.	.
<i>Cercocarpus montanus</i>	1/28	.	T/50	.	.
<i>Holodiscus dumosus</i>	.	T/100	5/75	6/80	4/33	12/100	.	.	.
<i>Jamesia americana</i>	.	T/50	3/75	.	.	T/14	.	.	.
<i>Pachystima myrsinites</i>	.	4/50
<i>Physocarpus monogynus</i>	7/5	.	T/25	.	.
<i>Prunus virginiana</i>	.	.	.	T/20	3/5	T/29	.	.	.
<i>Quercus gambelii</i>	.	T/50	.	1/80	17/100	13/100	26/100	20/100	11/100
<i>Quercus grisea</i>
<i>Quercus undulata</i>	T/5
<i>Ribes</i> spp.	3/100	.	3/50	1/60	7/39	T/28	T/25	.	T/50
<i>Robinia neomexicana</i>	.	T/50	.	.	T/44	T/43	T/75	.	.
<i>Rosa</i> spp.	.	.	.	T/40	T/28	T/29	T/75	.	.
<i>Symphoricarpos oreophilus</i>	.	.	.	T/20	T/39	1/86	T/25	.	.
<i>Vitis arizonica</i>
Graminoids									
<i>Andropogon gerardi</i>
<i>Aristida arizonica</i>
<i>Blepharoneuron tricholepis</i>	T/25	.	.
<i>Bouteloua gracilis</i>
<i>Bromus richardsonii</i>	1/100	2/100	T/25	1/100	2/89	3/86	T/50	.	1/50
<i>Carex</i> spp.	.	.	.	T/40	T/5	T/14	.	2/100	3/50
<i>Carex foenea</i>	T/22
<i>Carex rossii</i>	.	.	T/75	.	T/28	.	2/100	.	.
<i>Elymus triticoides</i>	.	.	20/50	.	2/11
<i>Festuca arizonica</i>	T/33	.	6/75	T/100	.
<i>Koeleria pyramidata</i>	T/39	T/14	T/50	.	.
<i>Muhlenbergia dubia</i>	1/100
<i>Muhlenbergia emersleyi</i>
<i>Muhlenbergia longiligula</i>	6/5
<i>Muhlenbergia montana</i>	1/17	.	1/75	.	.
<i>Muhlenbergia virescens</i>	T/11	.	.	T/100	.
<i>Piptochaetium tumbriatum</i>
<i>Poa fendleriana</i>	.	.	.	1/40	1/67	T/14	2/75	.	T/50
<i>Poa pratensis</i>	.	.	.	30/60	T/5	T/14	.	.	.
<i>Schizachyrium scoparium</i>
<i>Sitanion hystrix</i>	T/44	.	T/50	.	T/50
<i>Stipa</i> spp.	T/11	.	1/25	.	2/50
<i>Stipa pringlei</i>	10/100	.
<i>Trisetum montanum</i>	2/100	T/100	T/75	3/80	.	T/29	.	.	.
Forbs									
<i>Achillea millefolium</i>	.	.	.	1/60	T/22	2/14	T/25	.	.
<i>Antennaria parvifolia</i>
<i>Aquilegia elegantula</i>	.	.	.	1/60	.	T/43	.	.	.
<i>Artemisia frigida</i>	T/56	2/100	T/25	.	1/11	T/14	.	.	.
<i>Artemisia ludoviciana</i>	T/44	.	T/75	.	.
<i>Brickellia grandiflora</i>	T/17	T/71	.	.	3/50
<i>Campanula rotundifolia</i>	T/5
<i>Chaptalia alsophila</i>	T/5	T/43	.	.	.
<i>Clematis pseudoalpina</i>	1/11	T/43	.	.	.
<i>Clematis ligusticifolia</i>	T/71	.	.	.
<i>Cystopteris fragilis</i>	.	.	.	2/80	T/5	T/29	.	.	.
<i>Dugaldia hoopesii</i>
<i>Erigeron</i> spp.	.	.	T/25	5/20	T/5	T/29	.	.	.
<i>Erigeron macranthus</i>	.	.	.	T/40	1/22
<i>Erigeron platyphyllus</i>	1/28	.	T/25	.	.
<i>Erigeron superbus</i>	4/100	T/50	T/50	.	T/17	2/14	3/50	.	.
<i>Eriogonum jamesii</i>	T/22
<i>Fragaria bracteata</i>	.	T/50	T/75	1/80	T/33	T/43	.	.	.
<i>Fragaria ovalis</i>	T/33	T/100	.	.	T/5	T/29	.	.	.

¹Occurrence of each species in each habitat type and phase is indicated by two values separated by a slash. The first indicates the mean coverage (in percent) per plot for the shrubs, grasses, and forbs. In all cases, however, the first value is the mean for only the plots in which the species was present. The value to the right of the slash is the constancy for each species in the habitat type or phase; it is the percentage of the total number of plots in the group in which the species was found. In cases where a species had less than 1% cover, T is used to the left of the slash. A dot indicates that the species was not found in a group.

Id Herbaceous Species by Habitat Type and Phase'

ABCO/ACGR HT		ABCO/ELTR	ABCO/ACGL	ABCO/Sparse	ABCO/JUMA	PSME/QUGA HT		PIPO/QUGA	PIPO/QUUN HT		
ACGR typic P (N = 3)	HODU P (N = 3)	HT (N = 4)	HT, HODU P (N = 17)	HT (N = 1)	HT (N = 4)	QUGA typic P (N = 9)	HODU P (N = 6)	HT (N = 2)	QUUN typic P (N = 7)	MUDU P (N = 8)	MULO P (N = 2)
4/100	22/100	.	11/94 T/18	.	T/25 T/50	.	1/17
.	7/100	T/100 8/75	13/94 5/47 T/24	5/100	.	T/33	T/17 3/100	T/50	T/14	T/25	.
.	T/33	.	1/29	T/100	.	.	T/17
.	T/33	.	1/41	.	T/50	T/11	T/17	.	7/14	.	.
1/100	3/100	T/100	4/82	T/100	15/75	14/100	21/100 1/16	10/100	1/29 5/43 11/57	T/13 T/13 2/75	.
.	5/33	1/75	1/70	.	.	2/22	13/100
T/33	T/67	.	T/47 T/6	.	T/50 T/25	T/33 T/22	T/83 T/17
T/33	1/33	.	T/53	.	2/100	T/22	T/33
T/33
.	T/22	.	.	.	1/63 T/38	T/50 T/50 3/100
.	T/14	.	.
1/33	3/100	5/100	7/100	.	T/25	1/11 T/67 1/22	2/100	T/50	T/43	T/13 T/13	.
T/100	.	15/25 1/75 29/100 T/25 1/50	T/12 2/18 T/12	.	.	1/22	.	1/100	T/29	T/13	.
.	.	29/100 T/25 1/50	T/12	T/100	.	T/11
.	.	1/50	T/6	.	.	T/33 T/11	.	2/100	T/29 5/71 T/14	T/38 5/100 3/63	1/50
.	.	4/100	.	.	.	1/11 1/11	15/100
.
T/33	.	T/25	1/6	.	T/50	T/67	T/33	1/100	T/14 2/71 T/14	2/88	27/100
.	.	T/25	T/18	.	3/25	.	T/17	.	T/57	.	.
.	.	T/50	.	.	2/25	.	.	T/50	2/75	.	.
.	T/22 1/33	.	2/100 T/50	1/43 T/14	T/38	T/100
T/33	.	T/25	T/29	T/100	.	.	T/67	T/50	1/14	T/13	.
.
.	.	T/25	T/29	.	.	T/22	.	T/100	T/29	.	.
.	T/33	.	1/59 1/53	.	.	.	T/17
.
T/100	T/33	.	T/18	.	T/50	T/33 T/56	T/17 T/33	T/100 1/50	T/86	T/13	.
T/33	.	.	T/12	.	.	T/44	T/50
T/33	T/33	T/25	T/59	.	.	.	T/17
T/67	T/67	.	T/12 T/41 T/18 T/12	.	.	T/11	T/33 T/67
T/33	.	.	T/6	.	T/25	T/56	T/17	.	T/14	.	.
T/33	1/33	.	.	.	T/25	T/22	T/17	2/100	T/14	.	T/100
.	.	T/50	T/6	.	.	T/22	T/17
T/33	T/67	T/50	T/71 T/6	T/100	T/25	T/11 T/22	T/33 T/33	.	.	.	T/100
.

Species and Size class	ABLA/SESA	PIEN/ACGL	PIEN/ELTR	PIPU/FROV	ABCO/QUGA HT				
	HT	HT	HT	HT	QUGA typic P	HODU P	FEAR P	MUVI P	MUDU P
	(N = 9)	(N = 2)	(N = 4)	(N = 5)	(N = 18)	(N = 7)	(N = 4)	(N = 1)	(N = 2)
Forbs (continued)									
<i>Galium boreale</i>	.	.	.	1/20	T/33	T/71	.	.	.
<i>Geranium caespitosum</i>	.	T/50	T/25	1/60	T/55	T/29	T/50	.	.
<i>Geranium richardsonii</i>	T/56	T/50	.	3/60	T/50
<i>Heuchera parvifolia</i>	.	.	.	T/20	T/5	T/28	.	.	.
<i>Hieracium fendleri</i>	T/5
<i>Iris missouriensis</i>	.	.	.	1/80	T/5	T/14	.	.	.
<i>Lathyrus arizonicus</i>	.	4/50	T/25	1/80	T/33	T/29	T/25	.	T/100
<i>Ligusticum porteri</i>	T/100	T/100
<i>Lithospermum multiflorum</i>	T/11	.	T/25	.	.
<i>Osmorhiza depauperata</i>	2/89	T/50
<i>Oxalis alpina</i>	.	.	.	5/20	T/5	T/14	.	.	.
<i>Penstemon</i> spp.	.	.	T/25	.	1/5
<i>Pseudocymopterus montanus</i>	2/67	T/100	.	1/80	T/22	T/57	.	.	.
<i>Pyrola secunda</i>	T/78	T/50	T/25
<i>Senecio neomexicanus</i>	T/11
<i>Senecio sacramentanus</i>
<i>Senecio sanguisorboides</i>	7/100	1/100
<i>Senecio wootonii</i>	T/11	T/14	T/50	.	.
<i>Smilacina racemosa</i>	.	T/100	.	.	T/5	T/14	.	.	.
<i>Smilacina stellata</i>	T/33	T/50	T/50	.	T/17	T/71	.	.	.
<i>Stellaria jamesiana</i>	.	1/50	.	.	T/11	T/43	.	.	.
<i>Thalictrum fendleri</i>	.	T/100	.	T/40	2/61	T/86	1/25	.	.
<i>Valeriana</i> spp.	.	.	.	2/20	.	1/28	.	.	.
<i>Valeriana capitata</i>	.	.	.	15/20	.	T/28	.	.	.
<i>Vicia americana</i>	.	.	T/50	.	T/17	T/14	.	.	.
<i>Viola canadensis</i>	T/78	T/100	T/25

Herbaceous Species by Habitat Type and Phase¹—continued

ABCO/ACGR HT		ABCO/ELTR	ABCO/ACGL	ABCO/Sparse	ABCO/JUMA	PSME/QUGA HT		PIPO/QUGA	PIPO/QUUN HT		
ACGR typic P (N = 3)	HODU P (N = 3)	HT (N = 4)	HT, HODU P (N = 17)	HT (N = 1)	HT (N = 4)	QUGA typic P (N = 9)	HODU P (N = 6)	HT (N = 2)	QUUN typic P (N = 7)	MUDU P (N = 8)	MULO P (N = 2)
T/100	T/67	.	T/41	.	T/25	T/67	T/67	T/50	.	.	.
T/33	.	T/75	T/35	.	T/50	T/67	T/83	T/100	T/29	T/13	.
T/67	T/33	.	3/6	.	.	T/22	T/33
.	.	.	1/6	T/100
.	T/44	.	.	.	T/13	.
T/67	.	T/25	1/18
.	.	T/50	T/29	.	T/25	T/67	T/67	T/100	.	.	T/50
T/33	.	.	T/12
T/33	T/33	.	T/6	.	T/25	T/33	.	T/100	T/71	T/25	T/50
T/67	.	.	3/12	.	.	.	T/17
.	.	.	1/12	.	T/75
T/33	T/33	T/25	T/50	.	.	T/100	T/50
.	.	.	T/41	.	.	T/44	T/100
.
.	.	.	T/6	.	.	T/11
.	.	.	3/29	.	.	.	T/67
T/33	.	.	T/12
.	.	.	T/6	.	.	.	T/33
T/33	T/100	.	T/53	.	.	.	T/67
T/33	.	.	T/18	.	T/25	T/11	T/33
T/67	T/33	.	T/47	.	T/25	T/67	T/100
.	T/33	T/25	1/100	.	1/100	T/22	T/67
T/33	.	.	1/18	T/100
.	T/67	.	1/12	.	T/25	T/11
T/33	T/33	T/75	T/6	.	.	T/33	T/17	T/50	T/57	T/25	.
.	.	.	1/59

Alexander, Billy G., Jr., Frank Ronco, Jr., E. Lee Fitzhugh, and John A. Ludwig. 1984. A classification of forest habitat types of the Lincoln National Forest, New Mexico. USDA Forest Service General Technical Report RM-104. 29 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Vegetational data were collected from the Lincoln National Forest, New Mexico, to develop a forest habitat classification based on potential natural vegetation. There are 13 habitat types and, in addition, several phases identified on the Lincoln National Forest; 8 were previously classified by Moir and Ludwig (1979), and 5 by this study. The 13 habitat types represent 6 climax forest series: *Abies lasiocarpa*, *Picea engelmannii*, *Picea pungens*, *Abies concolor*, *Pseudotsuga menziesii*, and *Pinus ponderosa*. Each habitat type is described according to vegetation composition, topographical occurrence, soils information (when known), ecotones, adjacent habitat types, and general features.

Keywords: Forest vegetation, New Mexico, habitat types, plant communities, plant associations, forest ecology, and forest management.

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Rocky
Mountains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.



Southwest

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.



Great
Plains

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

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Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

United States
Department of
Agriculture

Forest Service

Rocky Mountain
Forest and Range
Experiment Station

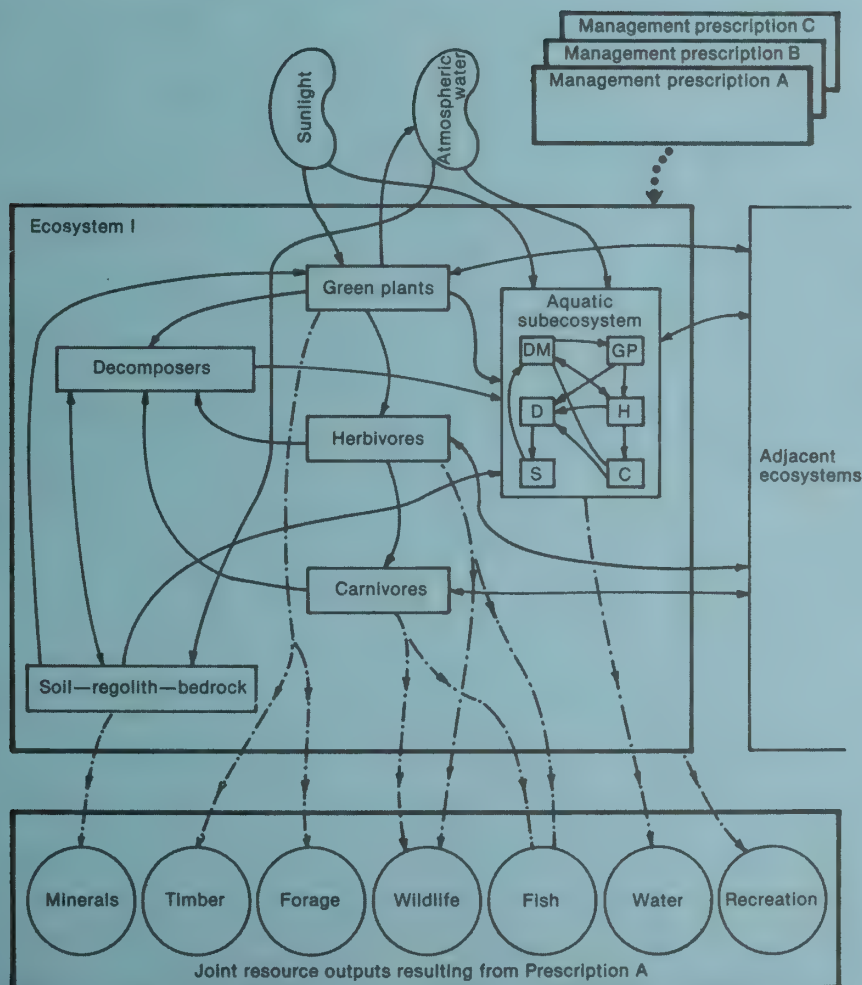
Fort Collins,
Colorado 80526

General Technical
Report RM-105



Estimation of Animal Production Numbers for National Assessments and Appraisals

Stephen A. Miller



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Estimation of Animal Production Numbers for National Assessments and Appraisals

**Stephen A. Miller, Wildlife Biologist¹
Maryland Department of Natural Resources**

Abstract

Population inventory methods and associated data are best applied in national assessments of wildlife and fish in conjunction with analytical approaches which utilize estimates of the production capability of the supporting habitat. Current knowledge of estimating animal population numbers is contrasted with current practice. Problems in using available population data as input for national assessments are reviewed.

¹Publication developed while author was wildlife biologist serving with the Fish and Wildlife Service, U.S. Department of the Interior, on IPA assignment from the State of Maryland.

Contents

	Page
NATIONAL ASSESSMENT IMPLICATIONS	1
INTRODUCTION	1
COMPLETE ENUMERATION	2
Territory-Mapping Method	2
Ground Counts	2
Extermination	3
Drive Counts	3
Remote Sensing	4
Aerial Survey	4
Thermal Infrared Scanners	5
Acoustic Methods	6
Temporal Census	7
CLASSICAL SAMPLING METHODS	7
Sampling Unit and Sample Size	8
Simple Random Sampling	8
Stratified Random Sampling	8
Systematic Sampling	9
Multistage Sampling	9
Multiphase Sampling	9
LINE METHODS	9
POINT METHODS	11
SPATIAL DISTRIBUTION METHODS	11
INDEXES	12
The Auditory Index	12
Pellet Counts	13
Track Counts	13
Roadside Counts	14
Miscellaneous Indexes	14
CAPTURE-RECAPTURE METHODS	14
Closed Populations	15
Open Populations	15
REMOVAL METHODS	16
Population Density Estimation	17
CATCH-EFFORT METHODS	18
Creel Census	19
CHANGE-IN-RATIO METHOD	19
BOUNDED COUNTS METHOD	20
LITERATURE CITED	20

Estimation of Animal Production Numbers for National Assessments and Appraisals

Stephen A. Miller

NATIONAL ASSESSMENT IMPLICATIONS

Agencies are increasingly expected to conduct wildlife and fish resource assessments and inventories as part of a broader multiresource approach. This trend is reinforced by two basic factors (Hirsch et al. 1979). First, because wildlife and fish resources compete with some other uses of the land, such as crop production, livestock grazing, and urban expansion, information about wildlife and fish must be comparable to information about these other resources in order to evaluate resource production tradeoffs resulting from various land management strategies. Second, multiple-resource inventories are more efficient than parallel, but separate, functional efforts.

A conceptual framework for assessing wildlife and fish resources should be based on the production capability of the habitat which supports a species or population. Using this approach, the habitat is described by the population level of a species either occupying or capable of being supported in that habitat. This approach also would help to greatly improve the ability to predict the quantitative effects of habitat changes on animal populations (Schweitzer et al. 1981).

There are basically two methods for determining the supportive capability of this habitat. The first uses knowledge of individual species/habitat relationships to develop models which predict the overall suitability of the habitat according to an appropriate rating scheme. This method interprets the potential production capability of the habitat. The second method uses statistical techniques to determine those habitat variables which are correlated with the abundance and distribution of a species. A prior knowledge of

species/habitat relationships is not required with this approach. The resultant models are designed to predict the production capability of the habitat in terms of the population numbers expected in the area.

Both methods require data on wildlife population numbers. To calibrate the habitat suitability index derived by the first method to the actual wildlife populations requires data on species abundance. The second method also requires data base related to species abundance and distribution.

Population estimation methods and associated inventory data appear to be best used in national assessments of wildlife and fish in conjunction with the analytical approaches described above. The individual states can and should provide much of this data.

Anyone who solicits or develops input regarding animal populations for national assessments should be aware of several problems with current and historical inventory information presently available. First, population density information is quite limited in scope. Thus, in turn, limits the number of species which can be considered in a national assessment. Second, much of the quantitative information on populations generally lack estimates of error. Without a standard error, there is no way to know how reliable the estimates are. Third, various animal population surveys have used less than optimal survey designs and techniques. The resulting population density estimates may be less reliable than estimates obtained using the newer techniques and analytical capabilities now available. Some of these are examined and discussed in this report.

INTRODUCTION

Davis and Winstead (1980) said that the methods used for estimating numbers of animals have evolved conceptually from simple counts to complex sampling programs and mathematical models, and that the technical calculations involved have progressed from pencil and paper to computer. There are many approaches to estimating populations, not all of which have been developed.

This review has three main objectives. The first is to present current methods for estimating wildlife populations focusing, where possible, on the following (Eberhardt 1978a):

- (1) Mechanics of the method (field and mathematical aspects).
- (2) Assumptions about the conditions under which observations are made.
- (3) Presentation of the formal model used with the method.
- (4) Such statistical aspects of the estimator as bias, efficiency, and robustness to failure of assumptions.

The second objective is to contrast the methods available for estimating animal populations with the methods actually in use. Literature was reviewed on completed research by the Divisions of Wildlife and

Fishery Ecology-Research and the Office of Cooperative Units within the U.S. Fish and Wildlife Service. Documentation from state projects done with federal aid also was reviewed. Documentation was solicited from the states for those projects which use techniques for estimating absolute or relative density as an integral part of the investigations.

The third objective is to evaluate the role of the methods for estimating populations and the role of the available data generated by these methods in national assessments of wildlife and fish.

COMPLETE ENUMERATION

The most direct way to determine the number of animals in a population is to count them all. Such a complete enumeration is called a census. Two types of censuses are recognized: (1) spatial censuses, in which a count is made of all the animals in a specified area at a specified time, and (2) temporal censuses, in which a count is made of all animals passing a particular place during a specified period of time (Overton 1971).

Territory-Mapping Method

One census technique is territory-mapping. This spatial method works on territorial species (i.e., occupy an ecological, if not a behavioral territory) which can be readily observed within their territories.

Standards for applying the territory-mapping method to bird census work were developed by the International Bird Census Committee (1970). This international standard was designed to alleviate problems of comparing the results of bird censuses obtained by different workers, in different habitats, or in different regions or countries. The Committee's report contains a discussion of the recommended procedural guidelines and data analysis processes.

Researchers using the territory-mapping method should state the population (or community) density as the number of stationary males (mapped territories) per 10 ha or per square kilometer.

The Michigan Department of Natural Resources, in cooperation with the USDA Forest Service, USDI Fish and Wildlife Service, the Michigan Audubon Society, and various other private citizens, uses a territory-mapping method to annually count Kirtland's warbler (*Dendroica kirtlandii*) singing males. Although the census procedure makes use of the behavior of male Kirtland's warblers to locate and count all the breeding males, it differs from the standard territory-mapping method in that only one pass through an area is made.

Spot mapping (Williams 1936) a variation of the territory-mapping technique. Ferris (1979) used the spot-mapping technique to examine the effects of Interstate 95 on populations of breeding birds in forest habitats in northern Maine. Numbers of breeding birds were determined on 12 study plots of 8 ha each, oriented at right angles to the highway. Each plot was censused along

four 400-m transects, spaced 50 m apart. Transects were marked at 50-m intervals, providing a grid to aid location of singing males. Censuses were conducted during morning hours from late May through early July 1975-1977.

Best (1975) conducted a controlled study, with known territories and population size, using the territory-mapping procedure. Results from his investigation indicated that the method provides highly variable (and, at times, only very approximate) estimates of absolute numbers, at least for dense populations of species with small territories. Best also identified two major inherent errors in this census procedure: (1) observational bias, resulting from variability in the identification skill of observers, observation conditions (weather, time of day, etc.), screening effect of the habitat, and conspicuousness of the bird species; and (2) interpretational bias, resulting from differing interpretations of census data. Another major difficulty that Best highlighted was the absence of reliable controls to enable estimation of the magnitude and direction of error.

Territory-mapping is normally suitable only for counting the stationary part of noncolonial, passerine bird populations during the breeding season. This does not include "floaters"—those birds which are nonterritorial in behavior and often comprise a substantial but variable portion of the population. This shortcoming led Dawson (1981) to conclude that, for a minority of species, if surveyed at the right time, the territory-mapping method may yield a good density estimate. However, the method generally gives an index, not an estimate, of density. An index is a measure functionally related to density, that does not yield an estimate. See the INDEXES section in this report for more details.

Ground Counts

Ground counts include a number of population estimation techniques that do not fit neatly under the organizational headings offered in this report. Most of these techniques involve complete enumeration by direct counts without the use of remote sensing apparatus. Because of the myriad of estimation approaches included under this heading, generalized comments about the mechanics and assumptions underlying ground count methods are addressed, where possible, in the discussion of each technique.

Ground counts are appropriate for species which are conspicuous and relatively sedentary (Eltringham 1973). Some species satisfy these criteria but still are difficult to count accurately. Large populations in limited spaces, as reported by Eberhardt et al. (1979), may significantly limit accuracy. They also had trouble counting seals because of individuals hidden behind rocks and bushes or ice ridges and because of the various hazards of terrain and parents.

Eberhardt et al. (1979) suggested that ground counts could be used to develop correction factors for improving precision of aerial counts. These surveys are addressed in the "Remote Sensing" section of this report.

A major disadvantage of using ground techniques, however, is that they are somewhat disruptive because they generally require entering the colony.

Playback recordings show great potential for use in censusing highly vocal species of birds which are otherwise difficult to detect and count (Marion et al. 1981). Because vocalizations often stimulate a response by nearby individuals, tape-recorded calls may be used to locate birds (or other animals) and may improve the efficiency of the count. Braun et al. (1973) used tape-recorded male challenge calls to locate male white-tailed ptarmigan (*Lagopus leucurus*) in Colorado. Broody females were located by playback of recorded chick distress calls. Effectiveness of the techniques varied with weather conditions, time of day, and time of season. However, the use of tape-recorded calls more than doubled the number of birds observed per observer-hour and reduced time necessary for the census.

Wenger and Cringan (1978) placed radio instruments on six coyotes (*Canis latrans*) to evaluate a census technique involving siren-elicited howling in Colorado. These coyotes were located weekly by radio signal and were subjected to an automatic, electronic siren stimulus. Three coyotes readily howled in response to the stimulus and were heard at distances up to 1.6 km. The investigators concluded that, before using the siren technique, average response rates for an area would have to be determined to qualify the accuracy of the census results.

Many ground count surveys are erroneously purported to be complete counts. In addition, small differences between survey results at different times often are treated as meaningful. In these cases, testing is important, because it can demonstrate that small differences in or from the data can be attributed to sampling variation, and are not statistically significant. Agencies which conduct "complete counts" of wildlife should consider using an efficient sampling system instead.

Extermination

In some cases, a census can be made in conjunction with the extermination of a population. For example, an outbreak of hoof-and-mouth disease among the Jawbone mule deer herd, in California, in 1924, led to the first absolute tally of animals over a large area in the United States, using the extermination technique. Leopold et al. (1951) noted that strychnine-poisoned salt was first used. However, because the poisoned salt was not entirely effective on winter ranges, hunters were hired to kill the deer.

Another example of census by extermination is the use of fish toxicants. The normal function of fish toxicants in fisheries management is to destroy unwanted fish. Although approximately 40 chemicals have been used for the destruction of fish populations, only two (rotenone and antimycin) appear to have been used in fish censusing. The use of poisons is limited to areas in lakes or rivers where water is relatively shallow or

slow-moving. Poisons are used in areas delineated by barrier nets placed across the channel of a river, across coves in a lake, or set out from a lake shore. In rivers, it is usually necessary to treat the water below the downstream net with potassium permanganate to destroy the toxicant and prevent any mortality outside the area.

The technique can give useful estimates of standing stock, presence of species, species composition, and strength of year classes (EIFAC 1975). The accuracy of the population estimate depends on the efficiency of collection of dead fish from the surface and bottom. In warm waters, kills are rapid, but accelerated decomposition of fish on the bottom may lead to an underestimate of the total number of fish killed. The cost of the technique may be low compared to other methods, although the use of a detoxifying agent increases the cost. Fry and juveniles are most difficult to collect, which may result in a serious underestimation of the population or biomass. The introduction of marked fish prior to poisoning may enable a correction to be made for fish not retrieved.

Platts et al.² report that explosion of primacord in small streams (up to stream order 4 or possibly 5) will kill almost all of the fish within 10 to 15 feet of the cord, provided that there are no major blocks between the explosive and the fish.

The stream area to be sampled should be blocked off with a net with mesh size small enough to keep young-of-the-year from leaving the area. Nets are needed to keep fish from moving out of the area while the grid is being laid, and to stop dead fish from floating downstream out of the sample area.

After each explosion, the dead fish are recovered by searching the stream channel. Most fish will be on the bottom. The streambanks must be inspected for occasional fish that are blown out of the channel. The net should not be pulled until the water clears, or at least until the water in the sampled area has had a chance to pass through the downstream net. The net should be inspected closely, because many fish will be caught in it.

Drive Counts

The drive count method evolved from the "deer drives" of pioneer days. This method uses counts of animals forced to leave a defined area by a traversing unit of "drivers" as the input for calculating population density estimates. The technique is usually modified for each particular area, but the procedures and features described by Overton (1971) provide a good general description.

- (1) Two crews of observers are required. One drives the animal out of the area; the other, stationed around the perimeter of the area, monitors animals leaving or entering the area.

²Platts, William S., Walter F. Megahan, and G. Wayne Minshall. 1981. Stream, riparian, and biotic evaluation methodology: Its design, use and value. Proposed for publication as a General Technical Report, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

- (2) The area must have boundaries that can be monitored. Each monitor must be able to clearly observe the boundary at least as far as the next monitor.
- (3) The monitors all look in the same direction around the boundary. Each monitor counts all deer leaving and entering the area between his post and the next monitor.
- (4) Each monitor stops counting as soon as the drive crew has passed his station. This ensures that only one observer tallies each animal crossing the line.
- (5) The drive crew lines up along one side of the area. The drivers then move through the area, keeping in line and in close spacing, driving the animals past the waiting monitors.
- (6) The total number of animals is then calculated as the sum of the animals leaving the area ahead of the drive crew plus the animals passing back through the drive line, minus the animals entering the area ahead of the drive crew and the animals passing forward through the drive line.

If the drive area is surrounded by a suitable dirt road, the tracks of animals crossing the road can be counted instead of using monitors. The low efficiency of this technique makes it unlikely to be widely used.

Remote Sensing

Aerial Survey

Aerial survey is a practical means of estimating the number of large animals inhabiting an extensive area (Seber 1980). To refine this technique, investigators have used three approaches: (1) considering accuracy to be a sampling problem, with the success of a survey rated according to the size of the estimate's standard error; (2) detecting how far the mean of survey estimates is displaced from the true population size; and (3) treating aerial survey estimates as relative, rather than absolute, measures of abundance (Caughley 1974).

Populations are usually surveyed from the air by counting animals on a strip of known width, from an aircraft flying a straight line, at a constant altitude above the ground. This technique, the strip-transect method, one of three variations of line methods commonly used to estimate animal populations, also is discussed in that context later in this report. The field of search is defined for the observer by two marks or streamers on the wing strut. Between these, the observer scans a strip of ground which is of constant and known width when the aircraft is at survey altitude. Population density is estimated as the number of animals seen on the strip divided by the product of strip width and the length of the flight line (Caughley 1974).

Visibility bias may affect the results significantly. Caughley (1974) maintained that the height and speed of the aircraft and the width of the field of search affect the efficiency of the observer, causing negative bias in aerial censuses. As the width of the field of search in-

creases, (1) the mean distance between an animal and the observer increases; (2) the time available to locate, recognize, and count an animal decreases; (3) the amount of eye movement needed to scan the strip increases; and (4) the mean number of obscuring items between the animal and the observer increases.

As cruising speed increases, the time available to locate and count an animal decreases, and the required rate of eye movement increases.

As altitude increases, the mean distance between the observer and the animal increases. Floyd et al. (1979) measured observability in an aerial census of deer in deciduous-coniferous habitat, in Minnesota. Testing the number of deer observed from the air against the known locations of radio-tagged deer, they found that approximately 50% of the deer were observed from the air.

Other influences on the efficiency of observers can be important sources of bias—in particular, boredom, fatigue, and time of day (Norton-Griffiths 1976). Boredom results in a decrease in awareness when an observer is searching a large unit without break. Fatigue develops as the census proceeds. Time-of-day has a number of effects. The increasing heat and turbulence around midday may lead to discomfort and air sickness. Erickson and Siniff (1963) found that air turbulence did not affect survey coverage, but may have affected the comfort and state of mind of the survey crews. The direction of incident light makes counting difficult early in the morning (Buechner et al. 1963) and late in the afternoon; towards midday the animals seek shade and become difficult to locate.

The construction and maneuverability of the aircraft used in aerial surveys, coupled with the experience of the pilot and observer(s), can significantly affect the precision of the estimates of the population being studied (Nichols 1980).

The Iowa Conservation Commission conducted an evaluation in 1979 of an aerial deer census technique over deciduous timber areas. Straight-line transects were flown over three study areas comprising 1,959 ha, using established landmarks and aerial photographs as reference. Outer limits of transects (200 m in 1978 and 400 m in 1979) were marked by a piece of tape on the airplane's wing strut.

Counts were made from a Piper Tri-Pacer³ airplane flying at 130 kph. Two observers were seated in the back and counted deer in the transect on each side of the airplane. A strip about 50 m wide, directly below the airplane, was not visible to either observer; therefore, deer in this area could not be counted. Counts were made only after a fresh snow of 8-10 cm, so that vegetation patterns could not be mistaken for deer.

Survey results indicated that the aerial survey technique is less variable in areas with higher population densities of deer. Because survey flights took place over a 3-week period, many deer moved into and out of the study areas. Failing to count a deer on low deer density areas has a much greater effect on mean number seen

³The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U.S. Department of Agriculture to the exclusion of others that may be suitable.

than failing to count a deer on a high deer density area. Also, movement of deer into or out of a small survey area with a low density of deer would have a greater effect on survey results than would such movement in a high density area.

Results of this investigation also indicated that both bright, sunny days and dull, cloudy days should be avoided when conducting an aerial survey of deer. There should be enough light to allow good contrast between deer and their background, but not so much that shadows are heavy.

Kushlan (1979) censused colonially nesting wading birds with helicopters because of their slow speed and excellent visibility. He found that censusing from fixed-wing aircraft provided poor data for many species, particularly for colonies of birds nesting within the tree canopy. Buckley and Buckley (1976) noted, however, that helicopters are believed by some to disturb nesting birds substantially. Eberhardt et al. (1979) stated that rotor noise apparently causes many marine mammal species to either leave haulout areas or to dive.

Kushlan concluded that helicopter censuses should be used if the level of disturbance is acceptable, the increased accuracy is needed, and if the colony sites and species present are suitable.

Caughley (1974) stated that the strongest influence on the visibility of animals from the air is the time available for scanning the census strip. He concluded that visibility was inversely related to the speed of the aircraft. However, the effect of time limitation could be circumvented by photographing the strip and counting the animals in the laboratory.

Photography is a considerable aid to aerial survey, and is used extensively to census large groups in open country. It is less efficient than the unaided human eye when cover is available to the animals. An observer can view an animal from several angles while flying past it. The camera takes one look from one angle and misses any animal obscured at that moment (Caughley 1974).

Norton-Griffiths (1976) stated that undercounting bias can be minimized by photographing all groups of animals containing more than some specified minimum numbers. Norton-Griffiths warns, however, that a visual estimate of group size should be made and recorded at the same time in case the pictures do not turn out well. Eberhardt et al. (1979) emphatically state that counts of marine mammals should be made from photographs whenever possible if sizable numbers are involved.

Ultraviolet photography has been used (Lavigne and Britsland 1974, Lavigne et al. 1975) to distinguish white-coated animals (harp seals (*Phoca groenlandica*) and polar bears (*Ursus maritimus*)) on backgrounds of snow and ice.

Eberhardt et al. (1979) discussed two techniques for obtaining correction factors to improve the precision of population estimates. One is to derive equations separately and then arbitrarily apply them in a census at a different time and locale. However, the correction factors may not remain constant over time and space. The second approach is to utilize part of the resources of the main survey to obtain the correction factors and to do so

as an integral part of the survey. In such a scheme, counts would be taken on a single area throughout the time that the main survey counts are made. The auxiliary counts should be spread throughout the time interval covered by the main survey and conducted in an area with enough animals present to reduce the effects of chance fluctuations of individual behavior.

One method for deriving correction equations as part of the main study is to conduct simultaneous aerial and ground counts of the same restricted areas. One of the most extensive applications of such a "ground truth" method is the waterfowl breeding ground counts cooperatively conducted by the U.S. Fish and Wildlife Service, the Canadian Wildlife Service, and various state and provincial wildlife agencies. Each year, more than 3.37 million km² of breeding habitat in Canada and the United States are sampled systematically to estimate the breeding population of 20 species of ducks.

Martin et al. (1979) describe the sampling scheme as a modification of a double sampling plan with stratification. A systematic sample of units is selected, with the first transect located randomly in each stratum. These transects are flown in fixed-wing aircraft at a height of 30.5-45.7 m above the ground; and all observed, identified waterfowl are counted for 1/8 mile (201 m) on each side of the aircraft. The number of birds is then counted on the ground within units comprising a subsample of the units in the aerial sample. The relationship between the air and ground counts for the subsample is used to adjust the much larger sample of air counts to a ground-count basis, accounting for birds on the ground that are not seen from the air.

The efficiency of this design depends on the relative cost of taking the two measurements, the strength of the relationship between the two procedures, and the variability of the estimates from each sample within a stratum. Martin et al. (1979) present examples of general applications of the design, including estimation of the population size for a particular species in a stratum.

Thermal Infrared Scanners

The potential for detecting and censusing big game by remote sensing of thermal infrared radiation emitted by the animals has long been recognized (Croon et al. 1968). Airborne, thermal infrared scanners have been used to detect white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*) (Reeves 1975). The technique is applicable to censusing open-range animals such as caribou (*Rangifer tarandus*), bison (*Bison bison*), pronghorn (*Antilocapra americana*), etc. (Croon et al. 1968).

Imaging infrared sensors are line-scanning devices which produce images closely resembling photographs. When mounted in an aircraft with the scanning direction perpendicular to the direction of flight, the forward motion of the aircraft and the scanning action of the optical system permit a large area of terrain to be scanned in a short time. As the field of view moves, a detecting device scans terrain objects of differing emittance or

reflectance characteristics and relays signals to the signal processing and display system. This system amplifies the relatively weak signals from the detector and then uses the amplified signals to produce a visible image (Croon et al. 1968).

Line-scanning systems provide a continuous recording of the spatial variation in average energy received from the total area within their instantaneous field-of-view. To be detected as different from its background, an animal must emit enough energy to produce an instantaneous response, averaged over the entire field-of-view, which is greater (or smaller) than the response produced by the background alone. This difference must be large enough to permit the signal processing system to discriminate between signals with animals and signals with no animals (Croon et al. 1968). The actual surface temperature of a deer at a particular time depends on a number of environmental factors: (1) air temperature, (2) solar radiation, (3) atmospheric water vapor pressure, and (4) wind speed (Parker and Driscoll 1972).

Consideration of thermal contrast between animals and other background components is an important factor in a general evaluation of this technique. Studies of deer detectability have been conducted almost exclusively in winter because of the high probability of snow backgrounds and the considerably reduced size of the geographic area which must be covered. Most modern scanners can detect deer from an altitude of 500 to 1,000 feet against a complete snow background (Reeves 1975).

Because the technique involves heat instead of visible light, scanning can be done at night, when animal activity is frequently greatest (Croon et al. 1968). Although overall thermal contrast is reduced during this period, it still may be sufficient for detection. However, as a practical matter, flying at low altitude in the dark is hazardous over much of the deer winter range because of rough topography (Reeves 1975).

The primary limitation of this technique is the inability of the radiation to penetrate vegetation. This precludes the use of thermal scanning for deer detection, in summer, in most areas of the U.S., because the animals tend to be on ranges with a tree overstory. Where the overstory consists of deciduous species, animals can best be detected after the leaves fall. Seasonal and diurnal habits of the animals may be used to advantage (i.e., movement of mule deer onto winter range areas; occupation of open yarding areas by white-tailed deer in the Northeast) (Reeves 1975).

Difficulties of distinguishing between animals of similar size is a major problem (Croon et al. 1968). Parker and Driscoll (1972) reported that interpreters made many errors when attempting to separate mule deer and pronghorn. The criterion for separating the species was the shading of the spots on the image. Because their temperature is higher and their size is larger, deer produced a lighter image than the pronghorn. Croon et al. (1968) suggests that a total count of mixed species may be useful, provided that the relative number of each species can be determined from ground samples. Graves et al. (1972) warn that false target

detection is a problem to the untrained interpreter. The infrared signal from large rocks sometimes appear warm in their study images at about the same intensity as the infrared signal from deer.

Flight altitudes must be considered as they relate to the size of the target to be detected. Parker and Driscoll (1972) failed to detect mule deer from an altitude of above 500 feet, whereas Graves et al. (1972) easily detected individual livestock during the summer, at a 1,000 feet altitude. The highest altitude that permits good detectability should be used, to maximize the area covered during each pass (Graves et al. 1972).

Wride and Baker (1977) listed the disadvantages of the technique for census of ungulates as (1) restricted use in severe terrain and southern latitudes, (2) inability to determine sex of animal, and (3) inability to separate species except when they are different sized animals. They found the cost is comparable to helicopter census work.

Thermal infrared scanning requires specialized expertise and sophisticated equipment. As with conventional aerial photographs, training and experience are necessary for proficiency in interpreting infrared imagery. The selection of a specific infrared detector depends primarily upon the general environmental conditions expected during the time of the survey and the specific type of target to be detected.

Currently, it is not possible to actually "see" small mammals with existing remote sensors (Reeves 1975). However, evidence of their presence by den construction activities and changes in the intensities of these activities also can be used to evaluate population dynamics (Reid et al. 1966).

Acoustic Methods

Acoustic methods for detecting fish were introduced in the 1930's and have been used consistently since then for estimating the abundance of fish. The method depends largely on interpretation of the signals from a calibrated echo-sounder.

Methods for processing signals include visual inspection and measurements from standard echograms, electronic integration of signals corrected for losses associated with different fish depths, and computer analysis of signals as recorded on magnetic tape. Computer analysis permits separate estimates for various depth strata and for several levels of amplitude.

If the population is sparse, echo counting based on "point" signals can be used. For high density populations, such as schools, a cumulative method using an echo integrator is more appropriate. If other sampling methods, such as netting, are used for calibrating the counts, then the estimates can be converted to absolute estimates of abundance (Seber 1981).

Winn et al. (1975) used a combination of acoustic methods and visual tracking to estimate the population of the humpback whale (*Megaptera novaeangliae*) in the West Indies. Population estimates were lower by the acoustic method, because only single adults call. Also

when a large group is calling simultaneously, it is difficult to distinguish individual calls. This is a distinct disadvantage of the acoustic method, in addition to the great expense of purchasing and installing the equipment. However, there are several advantages to the acoustic method—it can be used day and night, continuously or intermittently, in between other ship programs, and while other sampling is occurring.

Acoustic gear has been used successfully in deep freshwaters, but in shallow waters of both lakes and rivers, the methodology is less well defined. Identification or separation of species by acoustic means is not yet feasible (EIFAC 1975).

In addition to sampling errors, Seber (1981) outlines several operational and behavioral problems inherent with acoustic methods.

The FAO (EIFAC 1975) expects that the high cost of acoustic survey equipment will be reduced with advances in miniaturization, better knowledge of sampling requirements for given levels of precision, and the use of shore-based instead of on-board computers.

Temporal Census

As noted before, a temporal census is one in which a count is made of all animals passing a specific place during some interval in time. Temporal census techniques are suitable in the following situations (Overton 1971):

- (1) anadromous fish passing through fish ladders on dams,
- (2) birds entering roost sites, and
- (3) migrating animals using a well-defined route.

Fish traps are the simplest installations for counting and identifying migratory fish passing through fish ladders, because all fish moving upstream must go through the ladder. Automatic fish counters can be installed easily in fish ladders. Fish may be counted electronically, acoustically, magnetically, electromechanically, or optically. Installation of a series of automatic fish counters along river or stream systems is recommended to increase accuracy (EIFAC 1975).

Where site conditions permit, a fish barrier can be built across the full width of a river, allowing a complete count of the upstream and downstream migration. Otherwise, it still is possible to sample a portion of the run. Because of the cost involved, the use of devices employing fish fences extending across the full width of the river channel is restricted to smaller river systems and the tributaries of large rivers.

The roosting phenomena of certain birds can provide opportunities for using temporal census techniques, but the resulting estimates, at times, have proved quite controversial. Using counts of wood ducks (*Aix sponsa*) conducted during the autumn roosting flights as a population index, Hein (1965) and Hein and Haugen (1966) concluded that fall roosting flight counts could furnish an index which would detect changes of 15% in annual abundance of wood ducks. In contrast, Tabberer et al. (1971) concluded that flight counts in Louisiana were in-

valid because of variations in quality and stability of individual roosts. Smith (1958) felt that the technique in Louisiana was invalid because of yearly fluctuations in the amount of surface water in roosts.

Parr and Scott (1978) state that if a roost count is to be a valid index technique, the following assumptions must be met: (1) each roost must be a geographically discrete area containing an identifiable wood duck population separate from other roosts; (2) the number of wood ducks using a roost must reflect the general abundance of the species in the area, and the wood ducks must congregate at the roost solely as a result of their social needs, not because of the presence or absence of food or water elsewhere; (3) all, or at least a consistent proportion, of the wood ducks flying to a roost must be susceptible to being counted during any given counting event; (4) all, or at least a consistent proportion, of the wood ducks in an area must fly to identifiable communal roosts in the evening; and (5) there must be little unilateral interroost movement.

The temporal census approach can be used to estimate populations of animals which move or migrate seasonally. Extensive migrations of the gray whale (*Eschrichtius robustus*) between summer habitat off Alaska and the breeding lagoons near Baja, California, provide some unique opportunities for censusing. The migration route passes very close to the California coast, so that it is possible to attempt to count the entire population. A similar effort has been started for the northward migration of bowhead whales (*Balaena mysticetus*) into the Arctic (Eberhardt et al. 1979).

CLASSICAL SAMPLING METHODS

Estimation of population size by sampling techniques has several principal advantages over methods involving complete enumeration (Cochran 1977):

- (1) Reduced cost.
- (2) Greater speed. The data can be collected and summarized more quickly.
- (3) Greater scope. Surveys which rely on sampling have more scope and flexibility as to the types of information that can be obtained. Limitations on availability of trained personnel or specialized equipment may render a complete census as impractical.
- (4) Greater accuracy. Because only a portion of the total area or population is measured, greater care can be exercised in the measurements; supervision can be improved; fewer, but better trained personnel can be used; and the probable number of nonsampling errors can be reduced (Husch et al. 1972).

In wildlife studies, a two-stage process is often used in the survey design. The first stage is selecting sampling units that are representative of the overall study region in both space and time. The second stage consists of taking a sample on each unit in order to estimate the parameter(s) of main interest, usually abundance. Specialized methods, such as capture-recapture, removal,

line transects, etc. are used only at the second stage (Eberhardt 1978a). The complete enumerative methods outlined earlier also can be applied at the second stage to determine the abundance of selected subpopulations contained within the sampling units.

Sampling Unit and Sample Size

The determination of the optimum type of unit is important in the economics of sampling. A change in the type of unit usually affects both the cost of taking the sample and the precision obtained from it. The optimum unit is that which gives the desired precision for the sample estimates at the smallest cost, or the greatest precision for fixed cost (Cochran 1977).

Types of units should always be compared in terms of the kind of sampling that is to be used within the units, or, if this has not been decided, for the kinds that are under consideration. Changes in the method of sampling within units will change the relative net precisions of the different types of units. Unless one type of unit is uniformly superior, some compromise decision is made, giving principal weight to the most important criteria. Because it is seldom feasible to make a survey solely for the purpose of comparing different types of units, information about optimum type of units is usually a by-product of other surveys (Cochran 1977).

The decision about the size of the sample is important. Too large a sample implies a waste of resources; too small a sample diminishes the utility of the results. Cochran (1977) gives formulas to use in determining sampling intensity.

Simple Random Sampling

Simple random sampling is the fundamental selection method. Other sampling procedures are really modifications intended to achieve greater economy or precision (Husch et al. 1972).

Simple random sampling is a method of selecting a number of sampling units out of the population so that every one of the possible sampling units has an equal chance of being chosen. In practice, a simple random sample is drawn unit by unit. The units in the population are numbered from 1 to N . A series of random numbers between 1 and N is then drawn, and the units which bear these numbers constitute the sample. At any stage in the draw, this process gives an equal chance of selection to all numbers not previously drawn (Cochran 1977).

When a unit has been selected, it is not replaced, because this might allow the same unit to enter the sample more than once.

Cochran (1977) summarized the analysis procedures for the resulting data from the sampling units.

Stratified Random Sampling

In stratified sampling, the population is first divided into subpopulations. The purpose of stratification is to reduce the variation within the subdivision and to increase the precision of the population estimate (Husch et al. 1972). The subpopulations are nonoverlapping and together make up the whole of the population.

The subpopulations are called strata. When the strata have been determined, a sample is drawn from each stratum, the drawings being made independently in different strata. If a simple random sample is taken in each stratum, the whole procedure is described as stratified random sampling.

Stratification is a commonly used technique for the following reasons (Cochran 1977):

- (1) If data of known precision are wanted for certain subdivisions of the population, it is advisable to treat each subdivision as a "population" in its own right. (Husch et al. 1972.)
- (2) Administrative convenience may dictate the use of stratification (e.g., the agency conducting the survey may have field offices, each of which can supervise the survey for a part of the population).
- (3) Sampling problems may differ markedly in different parts of the population.
- (4) Stratification may increase precision in the estimation of characteristics of the whole population. The basic idea is that it may be possible to divide a heterogeneous population into subpopulations, each of which is internally homogeneous. If each stratum is homogeneous, in that the measurements vary little from one unit to another, a precise estimate of any stratum mean can be obtained from a small sample in that stratum. These estimates can then be combined into a precise estimate for the whole population. (Husch et al. 1972.)

Husch et al. (1972) cited the disadvantages of stratification:

- (1) The size of each stratum must be known, or at least a reasonable estimate must be available.
- (2) Sampling units must be taken in each stratum, if an estimate for that stratum is needed.

Strata can be selected on the basis of criteria such as topographic features, habitat types, etc. An arbitrary form of stratification is often used in sampling large areas where there is little basis for some kind of natural subdivision. In this case, the area can be broken into uniform-sized squares or rectangles, even though the resulting blocks may not contain homogeneous subpopulations. Still, it is reasonable to assume greater homogeneity within a smaller block than in the larger, entire area (Husch et al. 1972).

The different strata into which an area may be divided can be irregular in shape, of varying sizes, and of different importance. Stratification permits the sampling intensity and precision to be varied for the several strata. To estimate the number of sampling units needed, it is necessary to have preliminary information on the variability of the strata in the population, and to

choose an allowable error and probability level similar to the technique used for simple random sampling. With this information, the intensity of sampling can be estimated. The total number of sampling units can then be allocated to the different strata either by proportional or optimum allocation.

Cochran (1977) discusses the analysis procedures for data obtained from stratified random sampling.

Systematic Sampling

In systematic sampling, the sampling units are spaced at fixed intervals throughout the population but with some type of random starting point. Inventories using a systematic sampling design have advantages: (1) they provide good estimates of population means and totals by spreading the sample over the entire population; (2) they are usually faster and cheaper to execute than designs based on probability sampling, because the choice of sampling units is mechanical and uniform, eliminating the need for a random selection process; (3) travel between successive sampling units is easier because fixed directional bearings are followed, and the resulting travel time consumed is usually less than that required for locating randomly selected units; and (4) the size of the population need not be known, because every unit at a fixed interval is chosen after an initial random starting point has been selected. The sampling then continues until no further sampling units are found (Husch et al. 1972).

The primary disadvantage to systematic sampling is the lack of available methods for estimating sampling error.

The larger the area inventoried, the greater the amount of variation that can be expected and the more likelihood that a systematic sample will give a more precise estimate than a completely random or stratified random sample. The precision of a systematic sample estimate is better than that of a simple random estimate when the systematic sample contains more variation than is likely in the population (Cochran 1977).

Multistage Sampling

Multistage sampling is basically a means of working down to a sampling unit of manageable size (Lewis 1970). In multistage sampling, a population consists of a list of sampling units (primary stage), each of which is made up of smaller units (second stage), which, in turn, could be made up of still smaller units (third stage). A random sample would be chosen from the primary units. A random subsample of the secondary units would then be taken in each of the selected primary units, and the procedure would be continued to the desired stage. This procedure is called multistage sampling in general. Two-stage sampling, the most common application, indicates the sampling stops at the secondary stage. For example, an area to be inventoried might consist of numerous compartments that could be considered the primary

units in a sampling design. Plots chosen in the selected compartments would then form the secondary units (Husch et al. 1972).

Multiphase Sampling

The most used adaptation of multiphase sampling involves two phases and is often referred to as double sampling. In double sampling, an estimate of one variable is obtained by utilizing its relationship to another. The method is of most interest when information on the principal variable is costly and difficult to obtain, and the secondary and related variable can be more easily and cheaply observed. Thus, the aim of double sampling is to reduce the number of measurements of the costly variable without sacrificing precision of the estimate.

The general procedure in double sampling is that in a first phase a large random sample is taken of a secondary or auxiliary variable, X , which will yield a precise estimate of its population mean or total. In a second phase, a random subsample is taken from the previous sample, and on these sampling units, measurements are taken of the principal variable, Y . Note that the first and second phases are mutually dependent, because the measurements in the secondary phase are taken from a portion of the sampling units of the first phase. The result is a small sample on which both the auxiliary and principal variables, X and Y , have been measured. With these data, a regression can be developed between the two variables which can be utilized with the large sample of the auxiliary variable to make an estimate of the mean and total for the principal variable (Husch et al. 1972).

LINE METHODS

Line methods may be listed in three general categories: (1) line-intercept method, (2) strip-transect method, and (3) line-transect method.

The line-intercept method has been used by plant ecologists for many years. The method depends on the interception of an object by a line. Eberhardt (1978b), prompted by McIntyre's (1953) work on estimating plant densities, investigated the use of this method to estimate the number of den sites in a large, prairie dog (*Cynomys* spp.) town, in North Dakota. He suggested that the line-intercept method is appropriate in situations where detection depends mainly on the observer, such as with animals that do not respond to the observer's presence or with inanimate objects.

In the strip-transect method (also called the belt-transect method), counting is restricted to a strip of prescribed width. The simplest case of a strip transect is when the objects being sampled are readily visible and sufficiently abundant to permit using a restriction on width of the strip covered (Eberhardt 1978b). This method is widely applied during aerial surveys and was discussed earlier in that section.

Line-transect sampling has been used to obtain estimates of animal abundance since at least the early 1930's. The use of line transects may be considered a plotless method (Burnham et al. 1980). The observer traverses a sampling unit on a randomly selected straight line. Essentially, the same design consideration of line placement is needed in line-intercept, strip-transect, and line-transect sampling. Two distances may be recorded—one the direct distance to the object when it is first seen (the radial distance), and the other the distance from the transect to a line drawn through the object parallel to the transect (the right-angle distance) (Eberhardt 1978b). The sighting angle also can be recorded (Burnham et al. 1980).

Estimation of density can be based either on perpendicular distance or on sighting distances and angles. If sighting distances and angles are taken, the perpendicular distance can be computed after the data are collected. Valid estimation is not possible based solely on sighting distances; however, valid inferences can be based solely on perpendicular distances (Burnham et al. 1980).

Four assumptions are critical to obtaining reliable estimates of population abundance from line-transect sampling (Burnham et al. 1980):

1. Points directly on the line are never missed.
2. Points are fixed at the initial sighting position; they do not move before being detected, and none are counted twice. Movement is not critical if it is independent of the observer and "slow" relative to the observer's speed along the line.
3. Distances and angles are measured exactly, with no measurement errors or rounding errors.
4. Sightings are independent events. The flushing of one animal does not cause another to flush.

Basically, any convenient method of locomotion that will not violate these four fundamental assumptions can be used.

Mikol (1980) stressed the importance of understanding both the advantages and disadvantages of transect sampling when selecting a method to estimate bird population densities for a particular study. Some advantages are:

1. Transects can be used at any time of the year, and results for different seasons or months can be compared.
2. Each run of a transect on each transect line can be considered a sample replicate. In addition, if the line transect estimators discussed by Gates (1979) and Burnham et al. (1980) are used, sampling variances for the density estimates can be calculated.
3. Strip-transect and line-transect sampling are generally less time consuming and easier than other methods of collecting data for population density estimates (Emlen 1971).

Disadvantages of transect methods include the following:

1. The observer must be able to estimate all distances correctly (at least by distance intervals) for line transects or the data will not meet the requirements for data analysis.

2. It is difficult to determine the correct width of the belt in strip-transect sampling. A wide belt may result in incomplete sampling for some species, if there is a decrease in species detectability with distance. A narrow belt may also miss some species, especially those with large home ranges (Mikol et al. 1979). A narrow belt also has a very large edge relative to its area, which may result in a high variability of population estimates because of animals moving into and out of the belt.
3. The distribution of right-angle distances with line transects or, equivalently, the effective width, often will be different for different species.
4. An inaccurate estimate of population density may be obtained if the frequency histogram of right-angle distances for the data collected does not fit the distribution pattern required for the sampling method used (Gates et al. 1968). Some of the more recently developed data analysis methods do not require the data fit any particular distribution in order to obtain reliable results from line-transect sampling (Burnham et al. 1980).

Burnham et al. (1980) discuss the development of line-transect sampling and show a basis for the general construction of line-transect estimators. They developed the following line-transect density estimator:

$$\hat{D} = \frac{n\hat{f}(o)}{2L} \quad [1]$$

where the units of $\hat{f}(o)$ are the reciprocal of the units of the perpendicular distance x , L = line length, and n = number of animals seen.

Mikol (1980) provides guidelines for conducting transect studies for nongame birds to include aspects of study design, observer training, setting up transects, preparing field forms and maps, field sampling, and recording data.

The selection of a sample size requires advance information on the variability of \hat{D} as a function of the line length. Burnham et al. (1980) provide a discussion of the equations needed and provide an example for determining sample size when using line-transect sampling.

Numerous factors affect the probability of detecting objects, including weather conditions; the alertness, interests, and training of observers; habitat conditions; time of year; time of day; group size (for clustered populations); species; sex; and age. The problem most frequently encountered in applying line transects to wildlife populations is that animals move to avoid the observer. Such behavior tends either to increase the perpendicular distance of the animal from the line or cause the animal to be missed (see assumption number 2). Movement is less of a problem during aerial transect sampling. However, the inability to see all animals on the line becomes a problem with aerial transects (Burnham et al. 1980).

Two computer programs provide various estimators of density using the line-transect data: TRANSECT, developed by Laake et al. (1979), in conjunction with Burnham et al. (1980); and LINETRAN, developed by

Gates (1979). The availability, procurement, and documentation of program TRANSECT are discussed by Burnham et al. (1980). LINETRAN is a FORTRAN computer program that computes a variety of estimators (12) for the line-transect method of sampling biological populations. The characteristics of this program are discussed by Gates (1980).

The degree to which mobile populations can be surveyed by line-transect methods depends on the degree to which the inherent assumptions can be closely approximated. If the subject of the study is a highly mobile animal, serious problems caused by movement can arise, often to the extent of rendering line-transect sampling useless for such species. Populations which are routinely submerged underwater or are burrowed underground and those which assemble in loose groups and run, rather than flush, are not appropriate for line-transect methods (Burnham et al. 1980).

POINT METHODS

Ramsey and Scott (1979) presented an adaptation of line-transect methodology to circular-plot surveys. This technique was developed for surveying bird populations in rough terrain. The procedure consists of crossing the target region with a series of transects, along which stations are marked at regular intervals. An observer arrives on station, waits until the effects of his arrival have subsided, then begins a count which lasts a fixed amount of time.

For each bird detected at a station, its distance from the station is recorded. These distances are used to estimate the area which is effectively surveyed. This feature allows estimates of species density to be made.

The region surveyed around a station is viewed as a circular plot; however, all detections are recorded, so that the procedure is "plotless," like a line transect. As with line-transect methods, the total number of detections, divided by an estimate of the area surveyed, is the estimate of population density. The area surveyed acquires a very precise definition in terms of an effective radius of observation, which, in turn, is a well-defined parameter in the statistical model, summarizing an observer's inability to detect distant objects.

Ramsey and Scott (1979) identify several assumptions about the design parameters of this variable circular-plot survey technique:

1. The plot radius is large enough that all detection distances are below it.
2. Both the distance between transects and the distance between stations along a transect exceed twice the plot radius, so that no object is detectable at more than one station.
3. The pause time between arrival on station and count period is long enough to ensure that there is no effect of observer presence on the location or detectability of objects in the plot.
4. The length of count period is long enough to ensure that all objects within the immediate vicinity of the station are detected.

5. The count period is short enough to warrant the assumption that objects occupy fixed locations during the count.
6. No object is counted more than once at a given station.
7. The time between arrivals of observers is adequate to eliminate observer effects as in (3).

Szaro and Jakle⁴ assessed the applicability of the variable circular-plot method to riparian and desert scrub habitats and compared the results of using this method with those gained from the territory-mapping method. They concluded that the territory-mapping method is time consuming and requires more effort to census common bird species than the variable circular-plot method. Many of the rarer species, however, were not adequately censused by the variable circular-plot method. They stated that the advantages of the variable circular-plot method are that it (1) is not limited to the breeding season, (2) is usable in small habitat "islands," and (3) yields population density figures with an estimate of precision.

SPATIAL DISTRIBUTION METHODS

Several techniques have been developed which use the distances of individuals from randomly chosen points (closest-individual techniques) or the distances between neighbors (nearest-neighbor techniques) to calculate estimates of population density (Seber 1973). The background theory for these techniques is provided by Kendall and Moran (1963).

Distance methods can be used for animals which are relatively immobile and readily seen, or for well-marked colonies (Seber 1981).

Seber (1973) found that, because of sampling difficulties, and the present lack of supporting statistical theory, the closest-individual techniques are preferable to the nearest-neighbor techniques for estimating population density.

Distance estimators of density, which assume a randomly distributed population, may exhibit serious bias unless the population under consideration forms a completely random spatial pattern (Diggle 1975). This requirement severely constrains the usefulness of these methods (Andrewartha and Birch 1954).

Batcheler and Bell (1970) presented a method which utilizes both types of measurement for estimating the density of a random or of a nonrandom population. It employs the distance from each sample point to the nearest population neighbor, from that individual to the nearest neighbor, and from that neighbor to its nearest neighbor. The principle of the model is that an estimate of density is first obtained based on the distances from the sample point to the nearest population member. This point-distance estimate is then corrected for bias arising from nonrandomness by using the sums and frequencies of first and second neighbor distances.

⁴Szaro, Robert C., and Martin D. Jakle. 1981. Comparison of variable circular-plot and spot-map methods for estimating avian densities in desert riparian and scrub habitats. Poster paper presented at an International Symposium on estimating numbers of terrestrial birds held at Asilomar, Calif., October 26-31, 1980.

Diggle (1979) provided a review of the spatial point processes which have been suggested as possible models for point patterns in ecology. Because many of the methods are relatively new and untried, Diggle feels that firm conclusions cannot yet be drawn on the relative merits of the various methods.

INDEXES

Many management surveys provide only indexes to population levels. Eberhardt (1978a) defines an index as a measure that does not directly yield an estimated density (number per unit area) but that is functionally related to density.

The various indexes can be described as two distinct types (Overton 1971):

1. A count of animals, calls, or signs made in a manner which does not allow direct population estimate by application of sampling theory. This is a sample census without known sampling probabilities (e.g., roadside counts).
2. An estimate of the number of animals based on counts of some associated population. The method yields at one extreme a virtual tally of a population (i.e., track counts of quail in snow) and, at the other, indexes which are very difficult to calibrate (e.g., call-counts).

Indexes for estimating relative density are particularly useful in detecting changes over time or in comparing populations in different areas. However, if any comparisons are to be made, the surveys should be carried out under as nearly identical conditions as possible. Because changing conditions have different effects on different indexes of density, using more than one type of index is desirable (Seber 1981).

Where possible, replicated samples should be used for determining indexes, so that sampling estimates of variance can be calculated. Seber (1981) provides an example using roadside counts.

An index can be "calibrated" to account for the recognized effect of external variables such as weather or time of day (Overton 1971). Attempts to calibrate an index against some direct estimate of population abundance could be considerably complicated if the underlying relationship is not linear. Another complication is the bias introduced by sampling (chance) errors in both variables. In such a situation, ordinary regression analysis will yield a biased estimate of the slope, and therefore, result in a biased calibration equation (Eberhardt 1978a).

Eberhardt (1978a) stated that the coefficient of variation of many kinds of index data seems sufficiently constant in practice to supply an approximate guide for

planning purposes. For any particular locale for which an index is to be developed, prior data offer the best source for a variability estimate to be used in planning.

When such data are not available, or when a choice of methods is under consideration, Eberhardt (1978a) provided a useful table of population coefficients of variation that might be expected from various species. This table can be used for determining sample sizes to achieve a desired level of precision in the estimation.

The Auditory Index

Generally, the index of auditory signals of animal presence is constructed from data gathered by observers passing through an area, using standardized procedures concerning selection of route, starting and stopping time, number of stations per route and season of the year. Auditory activity, like other animal activity, is influenced by time of day, weather conditions, season of the year, mating status, and many other factors. Some procedures are attempts to adjust indexes for effect of such factors. The technique of multiple regression is well suited to simultaneous considerations of indexes and external factors of interest for predictive purposes.

The index developed from the mourning dove (*Zenaida macroura*) call-count survey is used as a guide in setting hunting regulations (Blankenship et al. 1971). More than 1,000 routes throughout the United States are surveyed annually between May 20-June 10. Each call-count route consists of twenty, 3-minute listening points at 1-mile intervals along roads. Records are kept of the number of doves heard calling, number of calls, and number of doves seen along each route. Analysis is based on doves heard.

Blankenship et al. (1971) demonstrated that stratification of these routes, based on Küchler's map of potential vegetation, resulted in a significant reduction in the error variance when compared with physiographic stratification (Fenneman 1931, 1938). They concluded, on the basis of statistical considerations, that the routes should be randomly selected within ecological strata, with the number of routes in each stratum presumably being inversely proportional to the variance (Gates et al. 1975).

Several studies have been designed to determine if call-count surveys could be utilized as indexes for breeding activity, eventual productivity, and fall population levels. Brown and Smith's (1976) analysis showed that call-counts probably were a valid survey technique for measuring population levels of white-winged (*Zenaida asiatica*) and mourning doves, and that the mourning dove call-count index could be used with reasonable accuracy to forecast early fall hunting success in Arizona.

Regression techniques can be useful for converting a relative index to an absolute density. Brown et al. (1978) showed that there is a potential to predict fall population levels of scaled quail (*Callipepla squamata*) from call-count surveys, as indicated by a significant linear relationship between the number of calling male scaled quail and hunting success.

Pellet Counts

Pellet-group counting is the process of estimating by fecal pellet-group counts, the actual or relative numbers of big game, or their days of use, in a given area (Neff 1968).

Plots are located in such a manner that the study area is adequately represented. Any of the sampling designs might be used. Then the number of pellet groups is counted in each plot and expressed in terms of pellet groups per unit of area. This expression is then divided by an assumed defecation rate to yield animal days utilization per acre for the study period. If the population is assumed to be constant, division of the latter index by number of days in the period yields the number of animals per acre (Overton 1971).

The chief advantage of this method is that pellet groups can be sampled by standard field plot techniques. Most pellet-group plots have been circles or long narrow rectangles, usually distributed in some form of stratified-random design. Sample plot layout often can be planned to minimize variance between plots or groups of plots (Neff 1968).

Pellet-group sampling is more efficient in areas of high pellet-group density. Winter ranges or other areas of concentration should be chosen for herd census or trend studies whenever possible (Neff 1968).

Daily defecation rates are needed for computing animal-days use or total numbers. Neff (1968) provides a summary of determinations of defecation rates for deer and other ruminants. High defecation rates in deer have been observed to accompany high feed intake, high forage moisture content, high percentage of young in the herd, change in diet from roughage to concentrates, and the impact of captivity (Neff 1968).

Observed differences in pellet deposition rates between male and female adult moose necessitate knowledge of the sex structure of a population when the pellet group census technique is utilized. This variation between the sexes complicates the technique and may preclude its use for moose in many instances (Franzmann et al. 1976).

Observer bias arises mainly from differences in interpretation and from missed groups. Because of missed groups, most counts underestimate actual pellet-group density. Missed groups error is influenced by plot size and shape, type and density of understory vegetation, and observer fatigue and inherent visual acuity. Sources of interpretational differences include decisions concerning peripheral groups, scattered groups, and the minimum number of pellets to be counted as a group. Common practice requires use of permanently marked plots which are periodically cleared. Temporary plots sometimes are used where the deposition period can be dated by reference to leaf-fall, by deformation of pellets caused by emergence of succulent feed, or by estimation of the period of herd occupancy of seasonal range. Such dating schemes introduce an additional source of observer bias (Neff 1968).

Pellet-group counts have been unworkable at times because of rapid loss of pellets through insect attacks or

heavy rains, because of difficulties in identifying pellets of different species, or because of extremely dense vegetation.

In a few cases, the pellet-group count has been tested against known numbers of deer in fenced areas, or against other census techniques. The estimates have been reasonably accurate in many cases (Neff 1968).

Track Counts

Track counts of species have been used extensively as indexes, but the development of an estimator of populations requires specific modeling of the relationship between number of animals and the spatial distribution and abundance of tracks.

McCaffery (1976) investigated the use of deer trail counts in Wisconsin as a population index and a means for evaluating fall deer habitats. Deer trails (defined as distinct paths in ground vegetation and forest litter caused by repeated use by deer) were counted along transects in spring, before greenup, and in late fall, before snow accumulation. Results of trail surveys correlated well with numbers of bucks harvested per square kilometer. When the variation in hunting exploitation between units is considered, agreement of these two indexes is remarkably close. A highly significant coefficient of correlation was produced when trail counts were compared with results of spring pellet-group surveys for those units where pellet counts were conducted within 1 year of the trail survey.

Linhart and Knowlton (1975) investigated the method of determining the relative abundance of coyotes (*Canis latrans*) using artificial scent stations in 17 western states. Each scent station line consisted of 50 scent stations, at 0.3-mile intervals, along a contiguous, 14.7-mile route. Each station was a perforated-plastic capsule containing a fermented-egg attractant placed in the center of a 1-yard circle of sifted dirt. Animal visits (based on tracks) were recorded for each station daily, for 5 consecutive days, during September, to provide an index to compare coyote population trends.

The data from each survey line were tabulated by subtracting the number of instances when scent stations were inoperative from the total of 250 station-nights (50 stations \times 5 nights) to give the total number of "operative station-nights." The total number of visits recorded for each species during the 5 nights was then used to calculate an index of relative abundance as follows:

$$\frac{\text{Total animal visits}}{\text{Total operative station-nights}} \times 1,000 = \text{index} \quad [2]$$

In addition to coyotes, the surveys have recorded the presence of domestic dogs, red wolves (*Canis rufus*), red fox (*Vulpes vulpes*), kit fox (*Vulpes macrotis*), swift fox (*V. velox*), gray fox (*Urocyon cinereoargenteus*), and a variety of noncanid carnivores—black bears (*Ursus americanus*), raccoons (*Procyon lotor*), ringtails (*Bassariscus astutus*), weasels (*Mustela* sp.), mink (*M.*

vision), skunks (*Mephitis* spp.), badgers (*Taxidea taxus*), domestic cats, mountain lions (*Felis concolor*), lynx (*Felis lynx*), and bobcats (*F. rufus*).

Linhart and Knowlton's technique was modified by Lindzey et al. (1977) to index black bear numbers in southwestern Washington. Their results indicated that the scent-station technique was a feasible means of indexing black bear abundance.

Roadside Counts

Roadside counts have long been a standard procedure for obtaining trend indexes in upland game. Roads are traveled for the specific purpose of counting the numbers of individuals of the species being censused which are then related to the number of miles traveled (Overton 1971).

An advantage of this method is that large areas are quickly and easily traversed in an automobile. However, factors affecting the roadside count include (1) activity of the animals as affected by hour of day, food supply, and weather, and (2) condition of the roadside cover. Activity may vary temporally, seasonally, and selectively. In addition, seasonal changes in cover use exist. The tall vegetation of late summer seriously impedes vision; the snow cover of the late winter enhances it (Davis and Winstead 1980).

Miscellaneous Indexes

Reid et al. (1966) investigated a method for approximating pocket gopher (*Thomomys* spp.) populations in western Colorado by counting new signs (mound and earth plugs) on high-altitude livestock ranges. New signs appearing in a 2-day interval and numbers of pocket gophers were counted on 54 plots (40,000 square feet each), during the successive fall seasons. There was a significant, positive correlation between the numbers of pocket gophers, determined by an intensive trapout of each plot, and the number of new signs appearing in the 2-day interval.

McCaffery (1973) showed that the number of white-tailed deer killed by traffic provides a useful index to changes in deer populations in Wisconsin. Road-kill trends correlated extremely well with trends in registered buck harvests. McCaffery concluded that only two ingredients are needed for a road-kill index: accurately reported road-kills and an estimate of percent change in annual traffic volume.

Gunson (1979) studied the use of spotlights to count deer. White-tailed deer and mule deer were counted during fall, on permanent transects, along secondary roads. The source of light was two, 200,000-candle-power aircraft landing lights mounted on the roof of a pickup truck. The driver and one observer each handled a light in a continuous operation on each side of the road. All observed deer were tallied, regardless of distance from vehicle. The preliminary results reported in this study suggested that pre hunting season counts of deer on permanent routes could serve as a useful index.

CAPTURE-RECAPTURE METHODS

Typically, in a capture-recapture study, the population is sampled two or more times. Each time, every unmarked animal caught is uniquely marked. Previously marked animals have their recaptures recorded, and then most or all of the animals are released back into the population.

Otis et al. (1978) classified capture studies by two schemes that are directly related to the class of models that are appropriate and the parameter that can be estimated. The first classification addresses the subject of closure—models can be classified as either open or closed. In closed models, the size of a population is constant over the period of investigation. White et al.⁵ subdivide the concept of closure into two components: (1) "geographic" closure (i.e., a boundary to limit the population), and (2) "demographic" closure to birth, immigration, death, and emigration.

The distinction between geographic and demographic closure is important, because open models can be subject only to demographic closure; geographic closure is still necessary.⁵

The second classification relates to the type of data collected. Two distinct types of information are provided: (1) information from the recovery of marked animals, and (2) information from comparing numbers of marked and unmarked animals captured at each sampling time.

Data from (1) can be used to estimate survival rates, whereas data from (1) and (2) both are necessary to estimate population size (Pollock 1980).

Otis et al. (1978) presented a review of the chronological development of conceptual approaches to capture-recapture and related experiments. They make it clear that any capture-recapture experiment requires that the researcher make specific assumptions concerning the many factors that affect the results of the experiment. The assumptions that are chosen determine which statistical estimation procedures should produce the best results from the data.

Pollock (1980) stated that the study design for studies of closed populations should be oriented around satisfaction of as many model assumptions as practically possible, so that a simple and reasonably efficient model can be used for estimation of the population. Traditional sample size calculations for a given precision, he noted, are only partially useful, because often the biologists must do a substantial amount of model selection after the study is completed.

Although sample sizes may be limited by practical problems, ideally a study should have approximately 10 sampling periods and constant capture probabilities averaging at least 0.2 for the whole study. This enables reasonable identification of the correct model and good precision of the population size estimator under that model (Pollock 1980).

⁵White, Gary C., David R. Anderson, Kenneth P. Burnham, and David L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Proposed for publication as a technical report of the Los Alamos National Laboratory, Los Alamos, N. Mex.

Closed Populations

The general assumptions for the closed-model, capture-recapture methods are as follows:

1. the population is closed,
2. animals do not lose their marks during the experiment,
3. all marks are correctly noted and recorded at each trapping occasion, and
4. each animal has a constant and equal probability of capture on each trapping occasion. This also implies that capture and marking do not affect the catchability of the animal.

The derivation of the formula associated with this method is introduced in many elementary courses in statistics as the "urn model," in which an urn contains N balls, M of which are black. A sample of C balls is then taken, and the number R , which are black is recorded. When an investigator is given M , C , and R and asked to estimate N , this variation leads to the Petersen-Lincoln Index estimator (Overton 1971).

Seber (1973) provided examples of the applications of the Petersen-Lincoln method to populations of underground ants (*Lasius flavus*) (Odum and Pontin 1961); snowshoe hares (*Lepus americanus*) (Green and Evans 1940); climbing cutworms (Wood 1963); redpolls (*Acanthis linaria*) (Nunneley 1964); and roe-deer (*Capreolus capreolus* L.) (Andersen 1962).

Otis et al. (1978) provide a unified approach to estimating parameters in capture-recapture experiments, which includes a statistical testing algorithm that allows the data to aid in selection of the "best" set of assumptions for the experiment. Although assumptions 1-3 must be made for all models considered, the focal point of their models and estimators is to relax assumption 4—equal catchability. They present a sequence of models each allowing for different combinations of up to three types of unequal capture probabilities: (1) capture probabilities vary with time or trapping occasion, (2) capture probabilities vary due to behavioral responses, and (3) capture probabilities vary by individual animal.

Otis et al. (1978) have developed a comprehensive computer program, CAPTURE, to compute estimates and test statistics for the various methods covered in their monograph.

It is appropriate at this point to compare the population estimates obtained through such state-of-the-art analytical aids with those derived from other closed population capture-recapture techniques routinely being practiced. Mares et al. (1981) tested the reliability of estimates obtained from several capture-recapture techniques (Lincoln-Petersen, Schnabel, and Schumacher-Eschmeyer methods) and the Least Squares Removal Method on a known population of eastern chipmunks (*Tamias striatus*). The population was composed of 82 individuals of known age and sex which were released on a 9.4-ha island previously devoid of chipmunks. With the exception of equal catchability, the experiment was designed to satisfy the assumptions of the above methods.

Point estimates always underestimated the true population size, and only the confidence intervals of the Lincoln-Petersen Method consistently included the actual population value. Least squares regression analyses suggested that the experimental population was composed of two groups of animals: those easily trapped and those hesitant to enter traps. As such, all population estimation methods estimated the easily captured portion of the population and underestimated the true size of the population.

In their conclusions, Mares et al. (1981) stated the need to develop estimation techniques that incorporate variable trap response by animals. Although the data necessary to execute the testing and model selection procedures included in program CAPTURE were not available in Mares et al. (1981), these authors indicated that they believed heterogeneity in capture probabilities was the important factor operating in their chipmunk population. Otis et al.^a, therefore, calculated a population estimate based on a model corresponding to such an assumption (Burnham and Overton 1979). The estimate obtained was identical to the known chipmunk population size, indicating the potential of an approach that allows choice of a model appropriate for a given experiment.

Open Populations

When live trapping is conducted over long time periods relative to the population dynamics of the target species, then "open" models become appropriate. In such studies, animals will be both leaving the study area (dying or emigrating) and entering it (being born or immigrating).

A tag-recapture experiment is conducted during which, on successive occasions, animals are captured from the population. The identity of marked individuals (or at least their recapture history) is recorded, unmarked animals are marked, and all (or some) animals are returned to the population. It is assumed that there are losses and additions to the population between occasions, so that there are three parameters of interest on each occasion.

Open models have a varying population size on each capture occasion and also involve survival and recruitment rates for each capture occasion. Burnham (1980) described the development of open models and discussed the steps used to determine capture probabilities. Cormack (1972, 1973) provides good supplementary explanations of the resultant Jolly-Seber model (Jolly 1965, Seber 1965).

Seber (1973) included assumptions for using this model.

1. Every animal in the population, whether marked or unmarked, has the same probability of being caught in successive samples, given that it is alive and in the population when the samples are taken.

^aPersonal communication from Kenneth P. Burnham, Team Biometrician, Western Energy and Land Use Team, U.S. Fish and Wildlife Service, Fort Collins, Colo.

2. Every marked animal has the same probability of surviving from the i^{th} to the $(i + 1)^{\text{th}}$ sample and of being in the population at the time of the i^{th} sample, given that it is alive and in the population immediately after the i^{th} release. Burnham⁶ adds that this assumption is also applicable to the "unmarked" animals or to an estimate of survival from marked animals applied to the whole population.
3. Every animal caught in the i^{th} sample has the same probability of being returned to the population.
4. Marked animals do not lose their marks, and all marks are reported on recovery.
5. All samples are instantaneous (i.e., sampling time is negligible).

The multirelease methods considered so far, although providing maximum information about changes in the population, involve much effort. Also, such multiple releases may be impractical or uneconomical, particularly in the study of commercially exploited populations.

A serious criticism of the Jolly-Seber model, according to Cormack (1979), is that, by including a separate parameter for each survival and each capture probability, it is too general. Any set of experimental observations contains a fixed and limited quantity of information about the system. The more parameters there are in the model, the more thinly the information is spread over them. The consequence with the Jolly-Seber model is that estimates are often found to have variances so large as to render them useless in practice.

A very important new development in open population models is the work of Jolly (1979).⁷ He reduced the large number of parameters by assuming a constant survival rate and/or a constant capture rate over the whole study. If these assumptions are realistic, the estimators are much more precise. Crosbie (1979) also considered these models, and developed a computer package to facilitate their use (Pollock 1980).

In the ecological literature, work is only beginning on a log-linear approach to open models (Cormack 1979).

Arnason and Baniuk (1980) discuss a computer system (POPAN) for capture-recapture data obtained from open populations and where marked animals are individually identifiable and classified according to various attributes (age, sex, species, etc.). The system edits and displays the data, provides general statistics-gathering capabilities, and provides a comprehensive set of analyses based on the Jolly-Seber models. Simulations by the system can help in planning experiments and in exploring sources of bias.

There has been an increasing opinion among modelers that "ball and urn models" are not applicable to real biological populations.⁸ This is because (1) capture probabilities vary in real populations because of differ-

ences in individuals and their responses to previous capture, and (2) there is no analogy in biological populations to the sides of the urn. This lack of analogy creates difficulties in interpreting what N means.

If closure is not true when using closed models, then substantial bias can result in estimating N . If, upon testing, the closure assumption is rejected, then an open model or partially open model may be preferable. However, more research is needed on these models.

REMOVAL METHODS

One way to avoid problems associated with variation in capture probabilities caused by behavioral response is to use a removal model estimator. In removal methods, only the first capture of an individual is used as a basis for estimation.⁸

In a removal study, in contrast to a capture-recapture study, animals are captured and removed from the population instead of being marked and released. On the second and subsequent visits, more animals are captured and removed. Continued sampling would catch progressively fewer animals on each occasion; eventually none would remain to be captured. The progressive decrease in captured animals is used to estimate the total number of animals. Alternatively, the marked animals can be released back into the population. In this way, they are "removed" from the unmarked population without having to physically remove them. This permits capture-recapture experiments to be used as if they were removal experiments.⁵

A hazard of removal studies is that they disrupt the population, and as substantial numbers of animals are removed, immigration may occur, violating the assumption of closure. Live trapping studies can minimize this violation if substantial mortality can be avoided (Otis et al. 1978).

Removal may be by killtrapping, electrofishing, trawling, or merely livetrapping the animals and physically displacing them to another area.

Conducting a removal experiment for purposes of estimating population size may sometimes prove more feasible than a capture-recapture approach. In such cases, the experimenter has available two classes of estimation procedures—the catch-effort techniques usually associated with Leslie and Davis (1939) and DeLury (1947) or the "removal" techniques first introduced by Moran (1951), refined by Zippin (1956, 1958), and generalized by Otis et al. (1978).

Otis et al. (1978) believed that their generalized removal method provides a better approach to estimating the size of a population than do catch-effort techniques, either because of the assumptions involved with the latter or because the concept of effort may be meaningless in many experimental situations. They warned, however, that the operating characteristics of the removal method are not completely satisfactory.

Removal methods are a special case of livetrapping methods; therefore, removal estimators can be used on livetrapping data. Otis et al. (1978) recommended that

⁷Jolly, G. M. Agricultural Research Council Unit of Statistics, University of Edinburgh, Edinburgh, United Kingdom. Mark-recapture models with parameters constant in time. Proposed for publication in *Biometrics*.

⁸Burnham, Kenneth P. Mark-recapture techniques for estimating animal populations—what has been done in ecology. Presented at the U.S. Department of Justice's special workshop: Research methodology in criminal justice program evaluation, March 16-19, 1980. Baltimore, Md.

livetrapping methods be used, if possible, because of the wider array of options available for the data analysis.

Population Density Estimation

The capture-recapture and removal models discussed involve only population size N as the parameter of interest. However, there may be interest in population density—the number of animals per unit area. To obtain true density values, the area that is being sampled has to be determined. Studies which have used the area enclosed by the sampling grid for population density estimation have resulted in severe overestimation. Such bias results from what has been called “edge effect” (i.e., not all animals have their entire home range within the trapping grid) (Otis et al. 1978).

Metzgar (1972) stated that the investigator seldom knows with certainty the true shape of home ranges sampled by means such as live-trapping or periodic observation. The locations at which the animals are recorded vary with the true shape of the home range, the way activity is distributed within the home range, the number of location records obtained, and the techniques for gathering these records.

Several approaches are given in the biological literature to solve this problem. Dice (1938) suggested that the area actually sampled by a grid of traps could be estimated by adding a strip around the grid equal in width to one-half the width of the home range of the species being censused. This is a good estimate of area sampled only if the grid is a neutral factor in the animals' environment. If the animals are attracted or repelled by the grid, the actual area sampled may not be directly related to size of their home ranges (Swift and Steinhorst 1976).

Two practical ideas for estimating unit area were discussed by Smith et al. (1971). The first involves marking the bait during a prebaiting period to determine the area in which captured animals were feeding prior to the beginning of removal (Adamczyk and Ryzkowski 1968, Gentry et al. 1971). The other method involves the use of assessment lines (e.g., Wheeler and Calhoun 1968).

The use of assessment lines is the most complex approach to population density estimation. Wheeler and Calhoun (1967), in designing a small-mammal census program, International Census of Small Mammals (ICSM), discussed the use of assessment lines to determine the area affected by a grid of traps or an octagon-shaped trap line. These lines extend from the census area into the border zone and are used to estimate the area actually sampled by the census grid or line. There should be some ambient rate (number per unit of linear distance) of catching marked animals along the assessment line. This rate should be a partial function of density, which in turn is determined in the border zone around the census grid or line by the effect of trapping on the census grid or line. The distances at which the rates of capture change will indicate the extent of the area of effect around the grid or line (Smith et al. 1971).

Gentry et al. (1971) tested the ICSM's octagon census method, Category 04 (Wheeler and Calhoun 1967). Early results from the work of Gentry et al. (1971) were instrumental in the designing and testing of a large, modified version of the octagon census method.

Another approach to estimating density has been to combine removal trapping with subsequent trapping on assessment lines to evaluate the area of effect of the original trapping. Smith et al. (1971) combined assessment lines with grid trapping, while Kaufman et al. (1971) trapped first on census lines and subsequently on assessment lines crossing them. In both cases, regression equations relating accumulated captures to distance along the assessment lines within the affected area are used in conjunction with similar regression equations developed from data taken outside the affected area to estimate the proportion of the population removed from the affected area. No objective method for locating the edge of the affected area is provided, however, and that determination will affect the final density estimates. In addition, Gentry et al. (1971) showed that, if there is reinvasion after the original removal, subsequent assessment line trapping may not reveal the limits of the affected area (Swift and Steinhorst 1976).

Spatial relations of the animals may be determined by using outer concentric squares of tightly packed traps (Smith et al. 1971).

Sarrazin and Bider (1973) provided a technique combining removal trapping with an estimate of the resulting decreased activity of the population that yields a density estimate. The technique of estimating population activity by checking fine sand transects for tracks every 2 hours may be too laborious for many applications, however (Swift and Steinhorst 1976).

O'Farrell et al. (1977) described two approaches to estimating the affected area of the trapping configuration from (1) the removal (actual or mathematical) of captured animals (Smith et al. 1971), or (2) captures of marked animals. The first approach assumes a constant population density across the study site, so that the change in the slope of the plot of capture location of unmarked animals delineates the actual area of effect. The same is true for removal trapping using snap traps. The assumption of constant population density also enters into the estimation of the proportion of animals removed from the area of effect for both the removal and mathematical removal procedures, because the average captures per station (or slope) inside the area of effect and the average captures per station (or slope) outside the area of effect are used to estimate the proportion removed. However, the second approach does not assume constant density and can be used only with live-trapping; it delineates the area of effect by means of captures of marked animals along the assessment lines. The ratio of marked animals to total captures adjusts the number of animals marked on the grid or census lines to include those animals that utilized the affected area.

Most of the available techniques for estimating population density have been developed for use with removal trapping. Removal trapping tends to alter normal move-

ment patterns and necessarily obviates following a given population through time. The assessment line technique is applicable to livetrapping and should work better than removal trapping (O'Farrell et al. 1977).

A live-trapping technique for population density estimation of small-mammal populations was described by O'Farrell et al. (1977). Two basic trapping configurations were used—a grid with assessment lines and two parallel census lines with assessment lines. An examination by O'Farrell and Austin (1978) of the density estimates obtained from each basic configuration shows that the two methods are comparable. They believed that the grid yielded more precise areas of effect because of the greater number of traps in a limited area. The grid also enabled the study of detailed home range movements, spatial relationships, and other aspects of small-mammal community dynamics.

The grid arrangement, however, had several drawbacks. There are more trapping stations, requiring more traps, time, and manpower. A grid with assessment lines yields the most information but represents such a major commitment in materials and labor that the ability to study replicate plots simultaneously is severely limited.

Census lines with assessment lines, in contrast yield the basic population measurements using less material and labor. Because this configuration requires less time and effort to establish, several replicate plots can be monitored simultaneously. If replicate plots are sampled within one habitat type, then mean densities and confidence intervals can be calculated (O'Farrell et al. 1977). If density is the measurement goal, they recommended the census line configuration, because it will yield values comparable to those obtainable by the more costly and time consuming grid arrangement.

Otis et al. (1978) advocate an approach to population density estimation for use with grid trapping which formulates the problem as one of joint estimation of density and strip width from data on one sufficiently large grid. Then, by denoting two or more subgrids of different sizes, those parameters can be estimated with a weighted, nonlinear, least squares procedure. This method requires much data to achieve satisfactory results. Both a large trapping grid and many captures are required. A carefully designed study is required to obtain reliable values of density and strip width; only rarely can a typical capture-recapture study be made to yield reasonable results.

CATCH-EFFORT METHODS

Catch-effort methods are based on the general assumption that the size of a sample caught from a population is proportional to the effort put into taking the sample. This means that one unit of sampling effort is assumed to catch a fixed proportion of the population, so that, if samples are permanently removed, the decline in population size will produce a decline in catch per unit effort. Such techniques, first used in 1914 for bears in Norway (Hjort and Ottestad 1933), are now widely used in the study of fish and small-mammal populations,

where effort is usually measured in such units as lines or traps per unit time (Seber 1973).

The following assumptions are associated with these techniques (Seber 1973, Davis and Winstead 1980):

1. The population is closed.
2. All individuals have the same probability of being caught during the period of collection of data.
3. The catch is proportional to the population. It is not a strict proportionality, except for short time periods over small amounts of effort. Rather, in general, catch is proportional to $N e^{-q \text{ effort}}$.

Ricker (1975) took exception to the first assumption listed above in regard to single homogenous fish populations. In this situation, he stated that when effort is proportional to rate of fishing, the catch per unit effort is proportional to the mean stock present during the time fishing takes place, whether or not recruitment from younger sizes takes place during that time. If the catch can be classified by size (i.e., age cohorts), then assume closure of exploited cohorts. Recruitment into nonexploited cohorts is irrelevant.

Ricker (1975) identified the following systematic errors in catch-effort methods:

1. Many populations have been found not to be amenable to this treatment, either because catchability varies with seasonal changes in environmental conditions or the animal's reactions, or because individual animals differ in vulnerability.
2. There may be day-to-day or other short term variation in catchability.
3. Recruitment and natural mortality, or immigration and emigration, can introduce serious error into these calculations, unless opposed tendencies happen to be in balance.

Ricker (1975) discussed the use of marked populations to check for significant departures from the conditions required for catch-effort estimates.

Dupont (1976) developed a catch-effort model which provides estimates of populations which are superior in accuracy to other catch-effort estimates to date. The assumptions underlying this model are:

1. The population can be divided into distinct cohorts.
2. The relative effort exerted at time t to catch members of a specific cohort is known. The probability that an animal from that cohort will be caught in a small time interval is proportional to Δt , to the effort exerted at time t , and to the cohort size at time t .
3. Some estimate of the cohort survival curves are available.
4. The probability of two or more deaths occurring in the interval is negligible compared to the probability of one death occurring in the same interval.
5. The catch from each cohort in successive time intervals is known.
6. The catches from different cohorts are independent. The probability of obtaining a given catch from any given cohort is unaffected by knowledge about the catch from other cohorts.

This method is designed for populations satisfying these assumptions or conditions: (1) heavy exploitation

by man or other predators; (2) the ages of individuals can be readily determined, and (3) some life-table information is known or readily available.

A computer program has been written to perform the computations inherent with this model.

Catch-effort methods are widely used to assess fish stocks around the world. When considering any fish-catching method as a sampling device, it is essential to know how effective the fishing gear is with respect to the quantity of fish caught and how closely the composition of the catch agrees with the composition of the stock. Variations in fish behavior and environment conditions present also cause differences in the efficiency of fishing gear used for sampling (EIFAC 1975).

The yield from traditional gear can be considerably increased by electrification. Electric fishing gear may serve to guide fish into traps, or the electrotoxic or tetanic effects of electric current can be used to capture the fish in some form of auxiliary fishing apparatus (EIFAC 1975).

The cost of collecting catch-effort data is often far less than that for comparable mark-release data. This is because species for which catch-effort data are obtainable are often already being exploited for commercial gain (or pest control). Thus to obtain catch-effort data, it is only necessary to record the activities of the harvester. Also, the problems which arise from the interactions between the observed animals and the data collectors (e.g., trap shyness, trap happiness) are considerably less serious for catch-effort methods than for capture-recapture ones (DuPont 1976).

Creel Census

In this technique, an enumerator roves through the fishing area interviewing anglers to determine the number n of fish caught and the time t expended. The interviewer is assumed to (1) start the trip at a randomly chosen point along a well-defined route which completely covers the fishery, (2) choose the initial direction at random from the two alternatives, and (3) travel at a constant rate of c circuits per day. If the catch rate n/t at time of interview is an unbiased estimator of an angler's catch rate for his completed trip, and, if the angler's movements relative to the interviewer's path never exceed the interviewer's rate c , then rn/ct , summed over all interviews, is an unbiased estimator of the day's total catch. The unit of time is one day, r is the number of times the angler was interviewed, and n/t is the catch rate at the r^{th} interview (Robson 1961).

Some distinctive features of the roving creel census are (1) the open end to the sample—the number of interviews in the sample depends upon the number and distribution of anglers present; (2) the sample of anglers obtained by following some rational route through the fishery constitutes a systematic rather than a random sample; (3) the probability of interviewing any given angler depends in some manner upon how long he fishes; and (4) only incomplete information is obtained for any one angler (Robson 1961).

The major weakness of the roving creel census is that the bias of estimation depends on the basic nature of the random fishing process, which generally is unknown. Unbiasedness of n/t implies that the waiting times to first catch and from first to second catch are identically distributed chance variables, and that all waiting times between successive catches have the same expected value. A variety of arguments could be made for unequal expected waiting times in violation of these conditions for unbiasedness, and the resulting bias could be of considerable magnitude. Robson (1961) suggested several ways of avoiding or minimizing this problem by making the creel census distribution-free, in the sense of an ordinary sample survey method.

Malvestuto et al. (1978) concluded that the roving creel method was sensitive enough to detect the size of changes in the quality of fishing in which managers were interested.

CHANGE-IN-RATIO METHOD

This technique basically requires a conceptual splitting of the population of interest into two exclusive and exhaustive components, using some criterion, such as sex or age class (e.g., juvenile or adult). Knowledge of the change in proportion or ratio of the two components before and after a known number of additions to, or removals from, each component specifies the initial size of each component. By sampling the population before and after the known additions or removals are made and obtaining estimates of the before and after proportions, estimates of the size of the population components (and hence total population size) can be produced (Otis 1980).

The following assumptions are made when using the CIR method:

1. Mortality rates for members of all disjoint components are the same.
2. All members of the population have the same probability of being sampled in each of the preremoval and postremoval samples.

Paulik and Robson (1969) discussed change-in-ratio (CIR) estimators for population abundance, productivity, and exploitation rates, and survival characteristics from observed changes in population composition.

Occasionally, an investigator is unable to classify correctly a significant proportion of the population into one of the two components originally conceptualized. For example, the researcher may originally intend to classify the animals in the preremoval and postremoval samples as either male or female. If the sampling is done by observing animals from a great distance, such as in aerial sampling, then it may be impossible to classify the young of the year accurately by sex. In this instance, categorizing the animals as either male, female, or juvenile (three disjoint components) would be more desirable. Otis (1980) presented a method for producing maximum likelihood estimates of each of the three population components in sampling experiments.

BOUNDED COUNTS METHOD

Regier and Robson (1967) suggested the following "bounded counts" method, based on the theory of Robson and Whitlock (1964). The underlying assumptions for using this method are that repeated counts are possible and that no units are counted twice.

Let N be the true number of units, and let N_m , N_{m-1} be the largest and the second largest counts obtained, respectively. Then N can be estimated by

$$\hat{N} = N_m + (N_m - N_{m-1}) = 2N_m - N_{m-1} \quad [3]$$

and an approximate 100% (1- α) confidence interval for N is

$$N_m < N < [N_m - (1-\alpha)N_{m-1}]/\alpha. \quad [4]$$

If s independent counts are made, then the bias of \hat{N} is of order $1/s^2$. For cases when more than two counts are made, Robson and Whitlock (1964) derived further corrections to reduce the bias (Seber 1973).

Seber (1973) suggested that this method could be applied in counting migrating fish-runs from a number of vantage points by equally perceptive enumerators or mechanical devices, and in small ponds, through which sieves may be drawn at least twice during an interval, when the population is closed.

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Population inventory methods and associated data are best applied in national assessments of wildlife and fish in conjunction with analytical approaches which utilize estimates of the production capability of the supporting habitat. The state of knowledge in estimating animal population numbers is contrasted with the state of practice. Problems inherent with available population data in regards to their use as input for national assessments are reviewed.

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526



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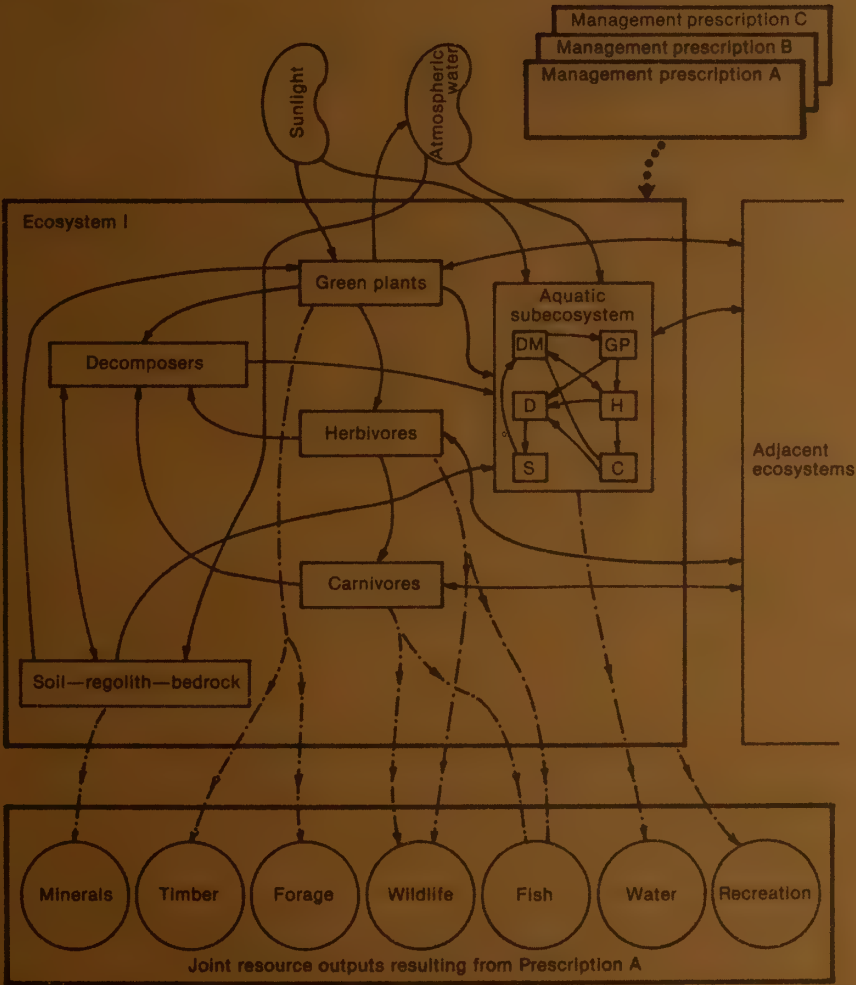
Rocky Mountain
Forest and Range
Experiment Station

Aggregate Timber Supply Analysis

Fort Collins,
Colorado 80526

General Technical
Report RM-106

Ralph J. Alig, Bernard J. Lewis, and Paul A. Morris



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Aggregate Timber Supply Analysis

Ralph J. Alig, Bernard J. Lewis and Paul A. Morris

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Aggregate Timber Supply Analysis

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CONTENTS

	Page
INTRODUCTION	1
SCOPE	1
ORGANIZATION	2
HISTORICAL REVIEW	2
COMPONENTS OF TIMBER SUPPLY ANALYSIS	3
1. LAND ALLOCATION	4
MODELING APPROACHES	4
ADDITIONAL MODELING CONSIDERATIONS	5
2. TIMBER INVENTORY PROJECTION	6
DIRECT METHODS	7
INDIRECT METHODS	9
SUMMARY	13
3. HARVEST FLOWS	13
SIMULATION TECHNIQUES	14
OPTIMIZATION TECHNIQUES	16
OTHER APPROACHES	18
INTEGRATION OF HARVEST FLOWS AND TIMER INVENTORY PROJECTION MODELING	21
SUMMARY	21
4. TIMBER INVESTMENTS	21
OPTIMAL CONTROL THEORY	22
RELATED APPROACHES	23
ANALYSIS OF INVESTMENT OPPORTUNITIES	24
OTHER MODELING CONSIDERATIONS	25
AGGREGATION AND UNCERTAINTY CONSIDERATIONS	25
OVERVIEW OF METHODOLOGY	27
LITERATURE CITED	30
APPENDIXES:	
APPENDIX A.—Major aggregate timber supply studies	42
APPENDIX B.—Timber inventory projection models by region	43
APPENDIX C.—Timber investment analyses by region	46
APPENDIX D.—Studies of retention and condition of timber investments on private lands	48
GLOSSARY	49

Aggregate Timber Supply Analysis

Ralph J. Alig, Bernard J. Lewis, and Paul A. Morris

INTRODUCTION

Aggregate timber supply analyses examine long-run trends in stumpage supply and identify opportunities for influencing the course of those trends through management of the forest resource. These analyses support the formulation and direction of public and private timber policies. In this report, aggregate timber supply analysis refers to techniques for analyzing timber resource supplies for geographic areas ranging from substate to national levels.

This paper presents a broad overview of major analytical techniques for aggregate timber supply analysis, and is intended as a reference document for analysts of natural resource supplies. It provides brief descriptions of major techniques and their applications, and includes critiques from those who have designed, used, or examined these techniques. Bibliographical references refer the reader to specific documents containing detailed operational information (i.e., computational structure, operating costs, etc.) for the cited analytical techniques.

Analyses of timber supply have been approached from a variety of perspectives; the objectives of a particular timber supply study and data availability dictate the specific analytical techniques employed. As a starting point, one might consider the physical quantity or "supply" of timber in a particular geographic region. At a given point in time a certain amount of wood fiber is present, and the growth and mortality within this timber base may be modeled and projected under different management assumptions and for a variety of future time periods.

The "physical supply" of timber is governed by both physical and biological factors that affect timber growth and mortality, while the broader concept of economic timber supply is based on economic feasibility of growing and harvesting timber. Economic timber supply is a schedule of the quantities of stumpage at different prices that producers are willing to offer for sale in a specific market area in a given time period under the existing institutional framework.² This definition of timber supply is adopted for use in this report. It is not synonymous with that for "physical supply," because it incorporates the notion of responses to different timber prices based on opportunity costs related to the management and availability of standing timber. As an example of this distinction, degrees of timber accessibility are more fully reflected by economic supply than "physical supply" estimates.

An additional influence on timber supply is the form of institutional and/or administrative constraints which

reduce the amount of timber from that which would otherwise be available from an economic standpoint. Parks and other areas withdrawn from the economically available timber base are a familiar example of institutional restrictions influencing timber supply. From an administrative perspective, constraints on timber production may take the form of targets for other forest outputs—wildlife, water, etc.—which must be achieved concurrently with the production of timber, thus reducing the economic timber supply.

The combination of all of the above factors complicates the analysis and description of timber supply. Furthermore, from the aggregate standpoint, often these distinctions may be lost in the actual process of data aggregation. If a given model fails to incorporate one or more of these distinctions, the validity and subsequent utility of its representation of actual timber supply becomes tenuous. However, the necessity for accurate information depicting timber supplies at all levels of geographic resolution remains. Marty (1969) summarizes the general utility of modeling timber supply from an aggregate perspective:

An aggregate timber supply model, using a classification of timber supply sources based on physical and economic characteristics and an intra-source projection technique which explicitly takes into account the more ultimate determinants of tree growth and removal, could be useful in predicting the supply response to various changes in economic conditions. The model would allow the analyst to estimate timber inventories under various assumptions about future prices and production costs. This information would provide an estimate of the change in total volume of stumpage that would become available under different future stumpage price expectations, thus providing a traditional long-run supply curve for timber. Similarly, it would be possible to estimate the effect on supply of changes in production cost factors like timber growing technology, labor costs, taxes, and so forth.

SCOPE

This report describes the major analytical techniques utilized in aggregate timber supply analyses that are available in published or mimeographed form; it excludes numerous techniques developed for proprietary use in private industry and other methods currently being developed. Techniques examined are almost exclusively those developed for use in the United States or Canada, which are generally representative of available techniques. Fries et al. (1978) provide examples of long-term timber yield modeling in other countries.

²Intended meanings of certain terms are defined in the Glossary.

Analytical techniques for describing aggregate derived demand for timber, based on society's demand for products derived in part from timber, are not considered explicitly in this report. Therefore, the topics of price formation and projection are also not discussed.³

Because physical, economic, and institutional factors act simultaneously to influence aggregate supply, their representation in current analytical techniques must be considered. However, a specific breakdown of models along these lines is impractical, because many modeling efforts incorporate each of these three factors to varying degrees within their analytical frameworks. The following approach for describing analytical techniques is adopted in this report.

Aggregate timber supply analysis requires incorporation of the following processes:

1. Projecting changes in the forest land base.
2. Sampling and measuring the forest inventory according to various criteria and assembling inventory information to facilitate monitoring of changes in various inventory strata.
3. Projecting the growth and yield of the timber resource, including its response to varying degrees of management.
4. Projecting timber removals.
5. Projecting timber investment potentials and strategies over time.

This report describes existing analytical methodology in terms of four of the above areas. The collection and organization of timber inventory data (item 2 above) is not discussed in depth but is considered whenever it is relevant to the other areas noted above. Accurate inventory information is a critical input to the design and effectiveness of timber supply analyses. While the distinction between assembling inventory data and subsequent analysis of the data is not always clear, in this report inventory data will be regarded as the information base which underlies supply analysis and allows it to proceed. Detailed discussions regarding the nature of inventory data and other timber supply data may be found in Clawson and Stewart (1965), Davis (1976), Tee-guarden (1977), Adams et al. (1979), Evans (1979), Eisenman et al. (1980), and USDA Forest Service (1981, 1982).

Institutional constraints in supply modeling are considered as they impact the forest land base and the establishment of output objectives (e.g., timber and water) from forest lands. However, techniques for analyzing supply in the presence of particular institutional harvest requirements (e.g., nondeclining even-flow) are only briefly addressed. Chappelle et al. (1976), Bell (1977), Johnson and Scheurman (1977), and Hann and Brodie (1980) examine some of the major techniques applied to analyze cases where these constraints exist.

³Aggregate "demand" studies have historically estimated consumption quantities rather than demand functions, analogous to production estimates versus supply functions. See Gregory et al. (1971) for a review of "demand" projection techniques and Adams and Haynes (1980) for an example of combined supply and demand modeling for price projection.

ORGANIZATION

The report first presents a historical overview of salient techniques that have been employed in analyzing aggregate timber supply. Current analytical techniques are then described according to four major component areas which contribute to aggregate timber supply analysis—land allocation, growth and yield changes of the timber inventory, harvest flows, and timber investment strategies. It is recognized that these components are not distinctly separate in theory or in their use in supply modeling. Such a classification does, however, permit the separation of areas in which specific techniques have tended to develop. This in turn facilitates the description of relative availability of methodologies and permits monitoring of progress of research in each of these four component areas. For each area, descriptions of specific models are provided as examples of current methodologies.

Following the discussion of modeling components, certain ramifications of data aggregation and uncertainty with respect to the reliability of timber supply projections are briefly explored, reflecting the fact that these aspects often seem to be inadequately addressed in aggregate timber supply studies. The report concludes with a general synthesis of relative strengths and weaknesses of existing timber supply methodology.

HISTORICAL REVIEW

Long-range studies of aggregate timber supplies in the United States originated with Hough's (1878, 1880) "Report upon Forestry" for the U.S. Department of Agriculture. Major studies that followed Hough's work are listed in Appendix A, which includes the date, primary analytical techniques employed, and scope of each study. Successive studies have in general been more comprehensive and reliable because of improvements in analytical techniques and data availability (USDA Forest Service 1982).

Quantitative determination of "growth and drain" guided major timber supply assessments (e.g., USDA Forest Service 1948) for most of the last one-hundred years. Difficulties inherent in rigid application of the "drain ratio" concept (ratio of current removals (harvest) to current growth) have been discussed by Vaux and Zivnuska (1952) and Bentley and Davis (1976), among others. For example, the drain ratio indicates changes in total volume of timber growing stock, but does not provide a measure of growth capability.

Until the latter half of this century, projections of aggregate timber supplies in published studies typically focused on physical measures such as growth, mortality, and removals, with little economic interpretation. The McSweeney-McNary Act of 1928 directed the Secretary of Agriculture to undertake comprehensive surveys of timber supplies to judge their capabilities in meeting timber "requirements" (Bentley and Davis 1976). Thus, USDA Forest Service studies under the McSweeney-McNary authority (e.g., USDA Forest Service 1948)

focused on a "balance of the timber budget of the United States," with maintenance of certain relative price trends of forest products.

One of the earliest systematic methodologies used for the projection of physical measures of aggregate timber supply was the stand projection method (e.g., USDA Forest Service 1965). Availability of computer technology and an improving data base in the form of relatively consistent timber inventory data facilitated the development and application of the Timber Resource Analysis System (TRAS) in the 1960's based on the stand table approach (Larson and Goforth 1970, 1974). Since then several other timber inventory projection techniques (e.g., individual tree based systems) have become candidates for use in regional timber studies; the major ones will be examined later in the section concerning timber inventory projection methodologies.

Economic measures of alternative timber supply levels were first used in the periodic USDA Forest Service appraisals in the 1970 Outlook (USDA Forest Service 1973). In this analysis, supply projections were based on balancing net growth and removals in the year 2000; utilizing this criterion, economically available supplies of softwood sawtimber were then estimated. The estimates of economic availability depended to a major degree on judgment rather than upon analytically derived relationships. Little attention was given to the timber management activities or total output level implied in a sustainable "net growth-removals" balance.⁴

The notion of supply and demand as schedules or functions (of quantities versus prices) was more thoroughly introduced into the decennial Forest Service assessments of timber supply in the 1980 Resources Planning Act (RPA) Assessment (USDA Forest Service 1982). Statistical analysis of the response of private stumpage supply to changes in prices and timber inventory levels was a basis for short-term harvest projections (Adams and Haynes 1980) in a comprehensive, interregional, economic equilibrium approach. In a different type of supply and demand analysis, the Forest Policy Project of the Pacific Northwest Regional Commission estimated private timber supply by maximizing present net benefits in conjunction with a downward-sloping curve for regional timber demand (Rahm 1981).

The gradual trend in aggregate timber supply analysis toward greater concern for economic variables was receded by several seminal papers in the latter half of this century. Vaux and Zivnuska (1952) stressed the use of supply and demand concepts from neoclassical microeconomic theory, thus focusing not on single quantities, but on price-associated functions. Gregory (1955) undertook further theoretical investigations concerning economic timber growth goals, and Vaux's (1954) construction of cost-efficient supply schedules for California sugar pine represented some of the earliest empirical work in this area (Bentley and Davis 1976).

Timber supply schedules based upon the theoretical cost-efficiency concept have been used in numerous

analyses since Vaux's 1954 study (Vaux 1973, Montgomery et al. 1975, Clawson and Hyde 1976, Jackson and McQuillan 1979). Use of statistically based modeling of aggregate timber supply trends has not been as widespread, in part because of problems with data availability. McKillop (1967), Adams (1974), and Robinson (1974) provide some of the earliest documented investigations of statistically based timber supply schedules. Use of statistical supply functions in a national timber assessment effort is documented by Adams and Haynes (1980), who also discuss integration of timber supply techniques within an overall supply and demand system that projects stumpage prices.

Duerr (1977) and Beuter (1979), among others,^{5,6} critique past national timber reviews and outline major problems to be resolved in future timber planning studies. Major criticisms of recent domestic supply projection methodologies have centered on problems in adequately addressing (1) growth and yield impacts of shifting timber management strategies over time, (2) responses of nonindustrial, private timber supplies, and (3) aggregation with respect to factors that might affect future timber availability.

In summary, aggregate timber supply analysis has progressed from studies guided by application of the ratio of timber drain (removals) to growth, to comprehensive supply and demand modeling that involves projection of stumpage prices. Before the 1970's, projections of aggregate timber supplies typically consisted only of physical measures. The relatively recent modeling of timber supply and demand equilibrium has included statistically based stumpage supply schedules, with feedback mechanisms linking stumpage supply and timber inventory. Major criticisms of recent aggregate timber supply studies have been directed at the modeling of the dynamics of timber investment opportunities and investment behavior on nonindustrial, private lands, and also at aggregation schemes that impede disaggregation of results, provide uneven representation, and are difficult to use as a basis for policy formulation.

COMPONENTS OF TIMBER SUPPLY ANALYSIS

Depending upon the objectives and degree of precision sought in a particular study, varying degrees of abstraction are involved in analyzing the complex interrelationships of socioeconomic, physical, and biological elements of timber supply. For expository purposes, four components of aggregate timber supply modeling are discussed in this report: (1) land allocation, (2) progression of the timber inventory, (3) harvest flows, and (4) long-term investment or management strategies.

⁵Critique assessment topic no. 1. Forecasting and RPA: 1980 RPA. By Dennis L. Schweitzer, Con Schallau, A. Schuler, Robert Stone, and Gregory Super, on file at USDA Forest Service Policy Analysis Staff Office, Washington, D.C. 1980.

⁶A critical analysis of timber supply research objectives for regional and national assessments. By John H. Beuter, on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 43 p. 1978.

⁴Problem analysis: Methods for analyzing national timber supply. By Thomas J. Mills, on file at Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 37 p. 1976.

Interrelationships among the four components are quite important given that, in theory, their dynamic interactions necessitate a simultaneous solution in modeling. The dynamic context of a time path of interconnected components implies that modeling the progression of aggregate timber inventories cannot be effectively achieved without considering the time path of the decision variables for land use allocation and management. Furthermore, the composition of future timber inventories and harvests is strongly related to present management.

While segregation of timber supply analytical tools by these categories allows for a more straightforward discussion (corresponding to their typically separate treatment in the literature), such a segregation should not obscure the interdependencies among these components. Furthermore, considerations of the linkages of the four components to the overall economy are important in analyzing timber supply patterns, although such relationships have seldom been examined in depth (Adams and Blackwell 1973). Many of the more useful techniques and associated assumptions for analyzing these four timber supply components will now be examined.

1. LAND ALLOCATION

The quantity, quality, and location of land that will be allocated to timber production have generally been estimated exogenously in aggregate timber supply studies, as have the related ownership patterns and objectives of management. For example, exogenous projections of commercial forest area have been used in estimating stumpage supply in the Timber Assessment Market Model (TAMM); such projections are based on observed trends and subjective judgment (Adams and Haynes 1980). While Adams and Haynes recognize that the acreage devoted to timber production or allowed to remain in a forested state is not independent of the timber price and growth projections made in TAMM, they conclude that the decisions involving the many possible uses of land are too complex for direct inclusion as endogenous processes in TAMM.

Some exogenous projections of land use, as in the TAMM approach, treat land allocation to timber growing as a "residual" use that is calculated by sifting out other uses of perceived higher economic value (e.g., agriculture), along with institutional uses (e.g., wilderness), from the total potential base for commercial forest acreage (Wall 1981). This approach does not allow for modeling the dynamic interaction between changes in the forest land base and relative timber stumpage prices.

MODELING APPROACHES

Burnham (1973) used a Markov land use simulation model to depict intertemporal land use shifts in estimating future United States cropland availability. Forest land was one of six land uses projected, based

upon land uses in the Southern Mississippi alluvial valley between 1950 and 1969. The finite Markov chain process involved estimating probabilities of land use shifts based on land movements between use groups over a historical time period, and then using these probabilities to project future land uses at alternative points in time. Projecting the future implications of past land use trends in this manner does mask the causative variables and, therefore, does not allow quantification of the processes underlying land use shifts.

In a study concerned with loss of wildlife habitat, MacDonald et al. (1979) also applied a Markov chain model to project bottomland hardwood acreages in the Lower Mississippi alluvial plain to 1995. Their probabilistic model was based upon historical land use data obtained primarily from interpretation of aerial photographs and other forms of remotely sensed imagery. Economic analysis in the study showed that agricultural crop production was more economically attractive than investments in natural bottomland hardwood stands or plantations.

Economic analysis of the allocation of land as an input or factor of production to timber growing has typically used the economic rent concept, with an unchanging alternative rate of return assumed for a particular forest ownership (e.g., Vaux 1973, Hyde 1980). Hyde (1980) applied the concept of land rent (i.e., net annual economic return per acre from a land use) to demonstrate the use of a variable land "production function." This function indicates land used for timber production at various prices and the associated efficient harvest levels. Hyde's land production function is based upon changing silvicultural technologies for each land class brought into production. As the various land classes receive different degrees of management intensity, different efficient yields per acre result. Access costs, dependent on distance to a site and topography, influence the degree of timber management applied to different land classes. This approach assumes that the landowner has a profit maximization goal, and that higher stumpage prices will attract less economically productive acres into timber production.

Access costs in timber supply determination are also addressed by Ledyard and Moses (1976) in a conceptual model of land use that combines transportation cost considerations (e.g., Bradley 1972) and capital theory. The model of land use in long-run, steady-state, competitive equilibrium is based upon economic principles described by Von Thunen almost a century and a half ago (Von Thunen 1966). Von Thunen's model allocated land to alternative crops based upon yielding maximum economic land rents, given crop prices and transportation costs to market. Ledyard and Moses extend Von Thunen's basic framework to model dynamic aspects involving interactions of time and transportation cost which have substantial implications for the use of capital in a forestry setting. Their focus, like Hyde (1980), is on a long-run, steady-state equilibrium rather than on identifying the path to equilibrium.

No forestry-based models currently exist with the capability for modeling interregional linkages in lar

allocation patterns involving forestry. A system for analyzing large-scale, interregional, agricultural land allocation, the Center for Agricultural and Rural Development (CARD) model, considers possible conversions of forest to cropland when estimating interregional shifts in agricultural production based on least-cost agricultural expansion to meet exogenous agricultural commodity requirements (Huang et al. 1981). However, the CARD model is presently not designed to estimate the possible reversion of cropland to forest.

GASPLY.—Georgia Supply (GASPLY) is an economic model designed to analyze forestry investments in Georgia (Montgomery et al. 1975, 1976; Robinson et al. 1978). The major theoretical bases of the GASPLY model—economic optimization procedures for land allocation models—are similar to those employed by Vaux (1973) and Hyde (1980). GASPLY estimates long-run equilibrium stumpage price and quantity and the associated total investment cost. Also estimated at this equilibrium point are the number of acres and owners involved, type of management (e.g., plantation) and location by planning district, and the site quality of the timber acreage. The criterion for GASPLY's economic optimization is maximizing present net worth of perpetual timber rotations.

The economic modeling of land use by GASPLY is based on the relative profitability of agricultural and timber production uses, assigning to a given land parcel the use with the highest economic rent (i.e., difference between all discounted relevant costs and revenues associated with production schemes into perpetuity). Limits are set on the amount of land that can shift between timber production and agriculture. Only the most productive timberland found in farmer ownerships is considered to be feasible for conversion to agriculture, while the amount of farmland available for conversion to timberland is restricted to idle farmland.

Idle land eligible for conversion to forest is assigned an opportunity cost (when calculating soil expectation value) equal to the economic returns that could be earned annually from alternative agricultural use of the land. Positive soil expectation values for timber production strategies cause such idle farmland to be converted to timberland in the GASPLY model. The agricultural opportunity cost is net of charges for clearing presently forested land, and the model allows for the possibility that idle farmland can revert naturally to timberland (i.e., custodial management). Similarly, land currently in timber production is shifted to agricultural use if associated soil expectation values are negative when alternative agricultural returns are considered.

Montgomery et al. (1975) recommend that commercial forest acreage of nonindustrial, private landowners be reduced in GASPLY input because of economically inoperable tracts (e.g., land around homesites). GASPLY adjusts land allocation patterns for expected population growth, with timberland shifting to urban-related land uses. The model can also reflect additional ramifications of urbanization, such as property tax changes. Impacted acres that are held in speculation (and will command high prices in the real estate market) are assigned

higher ad valorem property taxes that may render timber production uneconomical.

GASPLY can adjust forest types within the timberland base to reflect the possibility that the timberland will receive custodial care in lieu of plantation or intensive natural stand management (Montgomery et al. 1975). Custodial management implies no active timber management other than continued harvesting and protection against fire, insects, and disease. For acreage assumed to receive custodial management, GASPLY applies an adjustment to the pine and oak-pine types for hardwood invasion.

In summary, potential timberland acreage subdivisions are evaluated by GASPLY under three timber management intensities—pine plantation, intensively managed natural stand, or custodial—and the management intensity producing the highest present worth is chosen for that acreage subdivision or cell if it can exceed an accumulated agricultural rent. The selected timber management levels and associated costs and yields are assembled into a long-run timber supply curve, which indicates the various amounts of timber that can be produced at different average unit costs.

ADDITIONAL MODELING CONSIDERATIONS

The long-run supply curve is based upon the criterion of economic efficiency on the part of the timberland owner—i.e., maximizing economic returns through timber production. It also embodies major assumptions that owners have (1) perfect knowledge regarding future timber stumpage price levels, yields, costs, etc.; (2) perfectly competitive stumpage and input (factor) supply markets; and (3) no entry barriers for timberland investments (other than cost). Furthermore, no dynamic-adjustment paths (and associated costs and price changes) and spatial detail are generally considered. These assumptions underlie most economic maximization models of timber supply (e.g., Hoyer 1975; Jackson and McQuillan 1979, 1980).

Land allocation based on neoclassical economic efficiency principles guided Davis (1972), Dideriksen et al. (1977), Hidlebaugh (1980), and Shulstad and May (1980) in estimating potentials for the conversion of forest land to agricultural uses. The fact that many of these land use conversion or investment opportunities have not already been undertaken suggests that the behavior of the diverse class of private landowners is not fully explainable with current economic efficiency models and data. A host of other studies of the behavior of nonindustrial, private forest landowners support this proposition.⁷

Modelers in general have had limited success in projecting patterns of land use (Voelker 1975); this is particularly true in the case of nonindustrial, private land management. The forestry literature is replete with observations on a related phenomenon often termed the "small forest owner problem." Numerous proposals for

⁷*Problem analysis: Improving the timber productivity of non-industrial private forest lands. By J. E. deSteiguer, on file at Northeastern Forest Experiment Station, Forestry Science Laboratory, Princeton, W. Va. 37 p. 1980.*

attaining more "efficient" timber production patterns on these lands have been offered; some view this class of forest land owner as the key to significant increases in future national timber supplies (USDA Forest Service 1982).

The factors behind the apparent deviation of private landowner behavior from normative economic pathways have not been unequivocally identified, but may be the result of several combined characteristics of the market, owners, and analyses themselves. Imperfect market information, uncertainty, "noneconomic" goals, and lack of technical skills (Holley 1979) are examples of possible confounding market and owner-related factors. An important analytical shortcoming may be the present inability to account fully for all the relevant returns, especially nonmonetary benefits, and costs accruing to a landowner from alternative land uses.

This latter problem may arise primarily from data deficiencies and/or measurement errors; however, the analytical approach and theoretical foundations may also be partially at fault. In a study of New England landowner behavior, Binkley (1979, 1981) applied a "utility maximization" approach which accounted for the influence of some nontimber outputs in timberland management decisions. Boyce (1977, 1978) has also developed techniques for describing timber management activities in the context of multiple benefits. While these approaches have not been extensively tested, limitations to wider application in the short term appear to center on data deficiencies. The lack of accessible joint production data at aggregate levels, combined with inherent aggregation problems resulting from resource systems which have both varying ecological and economic bases, has greatly hampered aggregate multi-resource production analysis. Problems of even greater severity on the demand side further render integrated forest resource analysis a very difficult task at aggregate levels.

Deviations of timber suppliers from norms prescribed in the formulation of optimization models based on financial maximization prompted Marty (1969) to recommend a modeling technique adapted to multigoal or mixed goal analysis. His recognition of the difficulty of this task is still relevant today. While some progress has been made over the last decade, modeling problems related to incommensurable objectives held by many timberland owners strongly influence all four dimensions of timber supply analysis referred to previously. This contributes substantially to uncertainty in timber supply modeling (see section, Aggregation and Uncertainty Considerations).

Projection of land use allocation based on historical relationships among economic and other important variables is one alternative tool to complement economic efficiency models. However, few statistically based models of forest acreage trends have been employed, primarily because of substantial data problems. Adequate time series data for forest land use on which to base statistical functions are difficult to construct because of irregular measurements or estimates of commercial forest land in the past. Timberland acreages for

a particular state are estimated approximately every ten years by USDA Forest Service Forest Inventory and Analysis surveys (e.g., Knight 1973). Survey cycles differ among states. Attempts to augment periodic Forest Service forest acreage data with other major data sources is hindered by differing criteria used in past classifications of forest lands.

White and Fleming (1980) relied upon farm woodland data estimated every five years in the Census of Agriculture (e.g., USDC Bureau of the Census 1977) in analyzing factors underlying competing land use shifts in Georgia. A system of equations was statistically estimated to explain simultaneous changes in crop, pasture, and forest acreages. The most significant determinants of forest acreage were the amount of land in farms and farm crop acreages for previous years (Fleming 1980). Regression results were used in a simulation model to investigate the impact of government land diversion programs on land use patterns from 1980 to 2000.

In summary, the fundamental question of the allocation of land as an input to timber production has been analyzed using several distinct approaches in aggregate timber supply studies. National timber assessments have generally used exogenous estimates of timberland acreage, based on computations of forest land as a residual use (e.g., USDA Forest Service 1982). The dynamics involved in the joint determination of the timberland base and relative timber stumpage prices have not been modeled, nor have similar interactions with other sectors, particularly agriculture. In short, forecasting the availability and accessibility of forest acreage is a major problem in aggregate timber supply analyses.

2. TIMBER INVENTORY PROJECTION

A number of methods have been developed to project future levels of timber inventory (growth, mortality, accumulated stock, and structure) as it would occur in an unmanaged forest, as well as in response to certain management practices (Avery and Burkhart 1983). Such methods of projecting forest development can be divided into two broad classes—direct and indirect—based upon whether the method is applied locally to the same stand from which the data used for projection purposes are obtained (direct methods), or whether sample data for numerous stands are synthesized and then extrapolated to other stand conditions (indirect methods).

There are many models designed to project timber inventory development, some of which are outlined in appendix B. These models have been developed for numerous species and regions; however, models for single species may vary considerably, for example, in terms of the sample of stand conditions on which the model is based or the analytical methods employed. Evaluation of these models requires the synthesis of many quantitative and qualitative factors (Buchman and Shifley 1983). Surveys of inventory projection models are also provided by Williston (1975), Solomon (1977a,

Farrar (1979a), Dudek and Ek (1980), Burkhart et al. (1981), Moeur and Ek (1981), Trimble and Shriner (1981), and Hann and Riitters (1982).

DIRECT METHODS

Direct projection methods are those in which the results of operations performed upon a data sample are applied directly back to the population from which the sample was obtained, and only to that specific population. The most familiar of these methods is that of stand table projection, in which a sample of growth rates is obtained from a given stand and then applied directly back to that stand for projection purposes.

Stand tables are composed of frequency data showing number of trees according to such classification systems as species, diameter at breast height (d.b.h.), or height classes (Husch et al. 1972). Stand tables, commonly expressed on a per acre basis, are useful in depicting the stand structure or distribution of tree sizes and species in a stand. Stand table projection models use estimates of future diameter growth, removals, mortality, and ingrowth to adjust the stand table in an accounting fashion over time. Husch et al. (1972) further discuss the basis and the advantages and disadvantages of the general stand table projection method.

Although stand table projection models may be used to address localized, individual stand development questions, they have also been used for projecting aggregate timber supplies when forest-level or aggregate stand questions are being investigated. To answer these broader forest-level questions, the assumption is made that a large, regional inventory can be treated as one all-aged stand.

These generalized stand table projection models can use conventional timber inventory data and may be relatively simple and inexpensive to use. Some of their disadvantages are that they need a large data base, pose difficulties when different forest management schemes are being modeled, and are conceptually difficult to interpret. Another disadvantage is that, because the forest is modeled in aggregate, reliable tree size and distribution information for smaller areas is hard to extract. The following example of a stand table projection model expands on some of these points.

TRAS.—The Timber Resource Analysis System (TRAS) developed by Larson and Goforth (1970) has been employed as the inventory projection system for many recent USDA Forest Service timber assessment studies at the regional and national level (e.g., USDA Forest Service 1982). TRAS has continued to evolve since its inception in the 1950's, and an expanded version, TRAS-1980, is described by Alig et al. (1982). TRAS is a stand table projection model specifically designed to solve three types of problems: to reconcile differences among forest surveys, to update forest surveys completed at different times to a common compilation date, and to project long-term timber inventory changes.

The TRAS system includes both an exponential size class distribution model, the Q method, and a parabolic size class distribution function, the non-linear interpola-

tion method or NLI method (Larson and Goforth 1974). In relatively large aggregations of individual even-aged and uneven-aged forest stands, the overall stand table of number of trees by diameter class will approach an exponential distribution, for which the Q method is appropriate. The NLI method was designed to model the parabolic-type size class distribution of even-aged stands. Because collections of stands are modeled in aggregate, timber supply studies and such aggregates tend toward the exponential distribution (or the inverse J-shape as shown in fig. 1); thus, only the Q method or exponential distribution model is discussed in this report.

The Q method of TRAS is based on Meyer's (1952) observation that a graphical representation of the diameter distribution in any large forest area, with a mixture of stand sizes and ages, tends toward an inverse J-shaped curve (fig. 1). This curve is expressed as an exponential function that relates the number of trees per acre to their respective d.b.h. class. Thus, an average annual increase in diameter is related to a corresponding potential increase in the number of trees. This distribution seems to be generally true for the aggregation of even-aged, uneven-aged, or mixed stand distributions.

The aggregation capabilities of TRAS's inventory projection system depend largely on the assumption that aggregate "stands" constructed from a pooling of data from much smaller geographic subdivisions are an adequate representation of the combined smaller units, as gaged by the objectives and accuracy requirements of the particular timber supply study. In practice, TRAS is often applied to aggregates that represent millions of acres. Empirical verification of adequate representation by such aggregates is quite elusive because of the unavailability of independent and appropriate data bases upon which to check regional abstractions. Larson's test using South Carolina data did indicate that as few as ten Renewable Resource Evaluation sample plots were needed to construct a "sound" stand table for TRAS projections.⁴

The potential increase in inventory, due to growth of a stand, is computed as the annual per acre change in the number of trees in each 2-inch d.b.h. class (fig. 1). The overall change in inventory is obtained by subtracting the annual removals and mortality from the just-computed potential increase in the number of trees. This resulting number of trees added to the inventory is converted to a total volume by using the average volume per tree by d.b.h. class and the area of commercial forest land (Larson and Goforth 1974).

To prevent the development of unrealistically high inventory basal areas during projections, a set of constraint equations has been developed. As described by Larson and Goforth (1970), this set of equations reduces the radial growth and ingrowth and increases the mortality as the total softwood and hardwood basal area increases. The overall timber inventory in a region has generally been projected as two separate softwood and hardwood "average" stands by the TRAS model in aggregate timber supply analyses, although the projections of both stands are influenced by the total stand basal area constraint.

The mechanics of the TRAS projection system are relatively simple, and the accuracy of TRAS inventory projections essentially depends on the ability to adequately project radial growth, removals, and mortality, by diameter class, and by ingrowth.⁸ TRAS was designed to project timber management levels that are implicit in the radial growth, mortality, removals, and ingrowth data that comprise the bulk of the input to the stand table projection process (i.e., TRAS contains no growth, mortality, or removal rate coefficients internally). Thus, the implicit assumption behind the standard TRAS inventory projection is that timber management will be implemented at basically the same level over the projection period as that which formed the historically based stand table input. This assumption regarding projected TRAS parameters has been strongly questioned because of apparent trends in intensifying timber management to a degree different from that implied by standard TRAS projections.⁸

TRAS procedures were modified in the 1980 RPA Assessment to incorporate impacts of such management shifts (Barber 1980). The management shifts, based on identified timber investment opportunities, were translated into growth increments via Barber's modification of radial growth and mortality rates in TRAS's stand table. The modification procedure is of an ad hoc nature and was devised to fit an immediate need of the 1980 RPA Assessment modeling. The cumbersomeness and difficulty in monitoring involved in TRAS's modeling of

⁸Problem analysis: Timber supply analyses for RPA Assessments. By Darius M. Adams, on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 29 p. 1980.

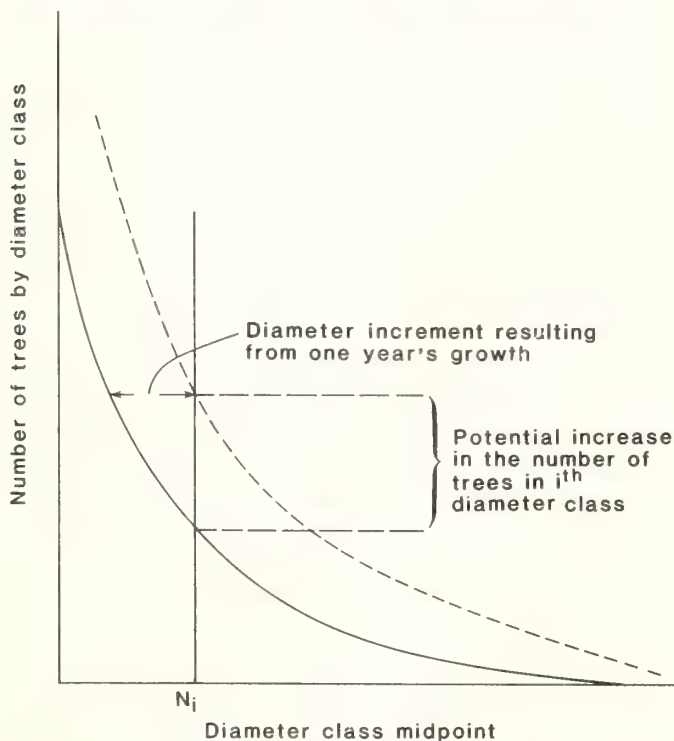


Figure 1.—Inverse J-shaped form of diameter distribution assumed in TRAS model for large forest areas with mixture of stand sizes and ages, with diameter distribution displacement shown for one year's growth (Larson and Goforth 1974).

shifts in timber management intensity is one of the major reasons that the USDA Forest Service plans to supplant it, at least in some regions where management shifts are significant, for the next major national timber supply assessment.⁸ This was prompted by the need to examine policy questions that frequently involve changes in timber management practices or intensity.

The use of TRAS to evaluate certain changes from the initial state over long projection periods has also been questioned.⁹ For example, in a shift from an inventory of predominantly old growth to largely young growth, such a transition could cause the lower d.b.h. classes to shift from predominantly suppressed to predominantly dominant crown classes. The corresponding acceleration in growth over time reflected by the TRAS model may not be an adequate representation of this change. The occurrence of such deviations from steady-state systems has led to suggestions that TRAS be limited to short-run inventory updates in some parts of the country.

Other reported limitations in the application of TRAS in some timber supply analysis tasks have seemingly increased with the marked evolution of timber supply modeling and associated needs in recent times. In part, some applications of TRAS extend beyond those originally intended in its design. For example, Row (1977) points out severe limitations of TRAS with regard to the previously mentioned insensitivity to trends in management levels and investment in timber growing activities, as well as environmental and multiple-use constraints. While noting that the TRAS system has been validated reasonably well in decade-by-decade biological projection of timber inventories for which it was designed, Row asserts that several major timber supply investigations (Adams 1975, Holley et al. 1975) have employed TRAS as a timber inventory projection module primarily because there was no other model available with adequate supporting data.

With respect to these criticisms of TRAS, the use of "average stands" to analyze broad regional areas has been regarded as acceptable when detailed input parameters for smaller areas are lacking or when there is no need to know how small parts of the total resource are changing with time (Oswald 1978). The basic assumption that a large regional inventory can be treated as one large, all-aged stand may be reasonable in some parts of the country. The assumption that a large, all-aged stand represents a regional timber inventory structure is questioned, however, when even-aged management is widely practiced and clearcutting is the accepted harvest method.

Two methods have been proposed to minimize the above weakness. One proposal is to divide the inventory into discrete strata and to use the TRAS model to project each stratum separately (Oswald 1978). The second proposal is to divide the inventory into discrete strata and to use the TRAS stand table projection technique for the older strata and to use a yield table projection technique for stands regenerated under more intensive even-aged management.

⁹Personal communication with A. R. Stage, USDA Forest Service, Moscow, Idaho.

Alternative approaches to the TRAS system for use in regional timber inventory projections include the Timber Resource Inventory Model (TRIM) and the Southern Pine Age-Class Timber Simulator (SPATS), models that currently are being developed and tested. The TRIM model employs a more disaggregated approach than TRAS, as it stratifies timberland acreage by age classes, site, species, management intensity, and stocking level (Tedder 1983). Acres can be shifted into different levels of timber management in two ways (1) pre-specified management shifts over the entire planning horizon or (2) management shifts based on economic investment behavior estimated internally by the model. Yield table projections for ten-year age classes for these different levels of timber management are made using an approach to normality technique.

The SPATS 5-year age-class model is intermediate between the TRAS and TRIM approaches in regard to level of aggregation. It can model three different forest types separately for the Southeast and Midsouth: (1) planted pine, (2) natural pine, and (3) oak-pine (Brooks 1983a). One average site class and stocking class are used and an approach to normality is also utilized to adjust for stocking variations. Reforestation practices can be directly simulated in the SPATS model, including estimating annual planting over a period by using equations developed using historical data (e.g., cost-share subsidies).

INDIRECT METHODS

Indirect timber inventory projection methods are based on a range of growth and/or yield observation samples that are utilized in estimating the parameters of projection models. The resultant models are then applied to subject stands larger in nature than those from which the original growth/yield data were obtained. In essence, therefore, these methods rely on a two-phase process: the first provides or describes the data to which the projection model is to be applied (i.e., the inventory stands or plots); the second sample provides the data for model construction, and for that reason it is more detailed than the former. The model is then applied back to the first sample for drawing inferences about the entire forest studied. Indirect models may be described in terms of two broad classes:

- A. Whole stand yield tables
 1. Normal
 2. Empirical
 3. Variable density
- B. Variable density growth and yield models
 1. Whole stand
 2. Size class and/or growth component
 3. Individual-tree
 - a. Distance-independent
 - b. Distance-dependent

Whole Stand Yield Tables

Yield tables describe stand development and yields by age, site quality, and, on occasion, other descriptors.

The most familiar examples of such tables are those described as normal yield tables, which attempt to describe the aggregate or whole stand yield of "fully stocked," undisturbed natural stands by site index and stand age. Such tables are constructed from measurements of many stands, but the stand characteristics are observed only at a single point in time; thus, they provide estimates of net production only (Curtis 1972). The pattern obtained by plotting yield or stand characteristics over age is assumed to represent a real growth pattern for stands of this density. While they have the advantage of being relatively easy to construct, this is generally outweighed by the fact that most normal yield tables are only applicable to relatively pure and even-aged stands, and they provide information only on aggregate stand variables. Such tables do not adapt well to management purposes, and they are also difficult to use for "non-normal" stands.

A variation on normal yield tables are empirical yield tables, which are constructed on the basis of average stand stocking conditions, as opposed to fully stocked stands. Such tables are constructed from sample plots with varying degrees of stocking, with multiple regression techniques generally utilized to determine average stand characteristics. While these tables allow for somewhat greater flexibility in projecting stand yields, they still do not overcome most of the difficulties stated above with respect to normal yield tables. Another important disadvantage of most such yield tables is that they provide relatively little information on stand growth. While yields are furnished for the "terminal" stand condition (i.e., end of the projection period), little information is provided on initial stand conditions and growth patterns that resulted in these terminal yields. This greatly reduces the utility of most yield tables for comparing management alternatives.

Variable density yield tables are the result of attempts to resolve these problems concerning growth representation in timber inventory projection modeling. Such tables provide yields for a range of stand densities for each age and site combination. However, early variable density yield tables were based on only single-point-in-time observations, and did not effectively provide further information on growth patterns. More recently developed variable density growth and yield modeling techniques reflect the incorporation of growth data from permanent plot records and corresponding equations to characterize forest growth as well as its integral forest yield. Variable density growth and yield tables have been geared primarily to silvicultural alternatives in forest management (Ek and Dudek 1980).

Variable Density Growth and Yield Models

Variable density growth and yield models are constructed to provide both growth and yields corresponding to different stand densities. They generally include specific growth functions, as well as yield functions derived from the integration and/or summation of growth functions. Such models may be utilized for the

construction of variable density yield tables, and thus they are of great value in contributing to the ability to represent potential results of different silvicultural management alternatives.

Whole Stand Models

These techniques have generally utilized differential equations to describe the rates of change of various components of stand development. An important initial study in this area was that of Buckman (1962), in which the growth rate of even-aged stands was expressed as a function of age, site, and stocking in a differential expression. With this approach, yields are obtained by integrating the growth rate equations over time. Depending upon the specific form of the rate model, differentiation may be employed to derive stocking levels which maximize growth.

Another significant study that exemplifies important elements of this approach was that conducted by Clutter (1963), in which growth rate models were developed and subsequently integrated to provide closed-form expressions for yield predictions. Data for this analysis were obtained from 5- and 10-year remeasurements of thinned permanent plots of loblolly pine. The first phase of the analysis involved the development of regression equations to predict per acre cubic foot and basal area yields from age, site, and basal area. Regressions for basal area growth and cubic foot growth were then used to obtain prediction equations for future basal area and cubic foot volume of a given present stand; this was achieved by integration of the aforementioned growth equations with respect to age. Sullivan and Clutter (1972) later revised Clutter's (1963) loblolly pine model and addressed two statistical problems: (1) dependent parameters within a system of equations and (2) observations from remeasured permanent plots that are not independent.

Size Class and/or Growth Component Models

Other techniques which utilize differential equations to model forest development may project growth components by size or diameter classes. Moser's (1974) system of nonlinear differential equations for predicting ingrowth, survivor growth, and mortality by diameter classes exemplifies this modeling approach (see also Moser et al. 1979). An additional example is the SHAF simulation model (Adams et al. 1974, Ek and Monserud 1979), based upon a stand table projection system modified to incorporate stand growth component equations given by Ek (1974) and later by Adams and Ek (1974).

Input for the SHAF model includes site index and number of trees by 2-inch diameter classes. Three components of stand growth by diameter classes are then estimated using nonlinear difference equation models. These components include ingrowth, upgrowth (i.e., number of trees rising from one diameter class to the next higher class), and mortality. Given these three

growth component expressions, the number of trees in each diameter class at the end of a given growth period may be obtained. By applying conversion factors to the number of trees in each diameter class, basal areas and volumes for each class may also be calculated. It should be noted that variations within different models may be manifest in different forms for components representing survivor growth, mortality, and regeneration.

Individual-Tree Simulation Models

A common characteristic of the preceding kinds of variable density growth and yield models is their reliance upon aggregate stand or size class characteristics such as basal area or number of trees for modeling of forest development. The most recent approach for modeling forest growth and yield consists of individual-tree simulation models, in which stands are described on the basis of characteristics of individual trees, which then may be combined to form stands. These models consider a set or list of individual trees and associated tree characteristics for a plot and simulate the growth of each tree by explicit or implicit "potential" growth functions; these, in turn, are modified by expressions reflecting tree size competition (Ek 1977). In this manner, tree spatial locations and individual tree characteristics influencing tree growth and resultant yields may be explicitly considered. Individual-tree models may be divided into two general classes: (1) those that are independent of intertree distances, and (2) those that require intertree distances as a necessary input (Munro 1974).

Distance-Independent Models.—Individual-tree distance-independent models do not require intertree distances but classify the competitive status of the subject tree by comparing its characteristics (size, crown ratio, etc.) in relation to all other trees in a sample plot. Each sample tree is weighted with an expansion factor to indicate the number of trees per acre it represents.

The advantages of this type of model are that inputs consist primarily of conventional inventory data (although some modifications are required); it can model any age structure or species mixture; and it provides relatively detailed information on tree and stand parameters and on the effects of stand management. Disadvantages of this kind of model include its relative complexity and the inability to predict the growth of specific single trees with any reliability (Munro 1974). It should be noted that all of the individual-tree models described herein are similar in that they involve some type of tree accounting, product conversion, and summary capability, with the actual stand dynamics treated by specific program sections or subprograms for survivor tree growth, mortality, and, sometimes, ingrowth or regeneration. Somewhat distinct from this dynamic part of the model, there may be subprograms for management activities, such as harvesting or thinning. Other models have identified specific options for insect and disease impact studies and habitat analyses.

Individual-tree distance-independent models have been employed to simulate growth and yield for in-

dividual forest stands, small forested areas, and for entire states. Criticisms are sometimes voiced, however, concerning the aggregation capabilities of these models as well as the potential costs of adapting them to such large-scale assessments. The extent to which the number of plots needed to represent forest conditions of interest would expand in moving from substate to regional or national timber assessments requires further examination, as does the attendant cost and accuracy of the resultant biological modeling. Conversely, an individual-tree model capable of projections for 20 species may be no more complex (and probably less so) to construct and use than 20 "simpler" models for 20 different species.⁹ The difficulties inherent in combining diverse growth and yield models are well known to resource projection analysts.

Individual-tree distance-independent models have been developed by Lemmon and Schumacher (1962), Botkin et al. (1972), Goulding (1972), Stage (1973), and USDA Forest Service (1979), among others. Two examples of this type of model are described below.

STEMS.—An individual-tree distance-independent model considered potentially useful for regional or national analyses is the Stand and Tree Evaluation and Modeling System (STEMS), formerly known as the Forest Resources Evaluation Program (FREP) (USDA Forest Service 1979, Hahn et al. 1979, Moeur and Ek 1981). STEMS is a forest growth model designed to describe stand development, with or without management activities. The model's timber growth projection system has been applied in the Lake States (Smith and Raile 1979, Jakes and Smith 1980) and is being tested in the Pacific Northwest; plans exist to calibrate it for use in the Central States and Southeast as well.

STEMS will handle a variety of forest conditions including pure or mixed stands. Growth and yield for even- and uneven-aged stand conditions can be simulated if the relevant biological response equations have been developed and tested for the particular geographical area. STEMS can be used to (1) update or project plot tree lists to a future time, or (2) evaluate various silvicultural management alternatives. The model has numerous timber management options available.

STEMS uses basic inventory data or data from other sources such as stand and stock tables to construct an input list of individual trees representative of the forest condition of interest. This tree list contains species, diameter at breast height, crown ratio, and an expansion factor (per acre) for each tree. If crown ratio is missing from the input list, it is approximated by using a relationship with diameter and basal area.

The model's operational portion, which uses growth equations for individual trees to transform the input tree list into an updated output tree list, has three parts: potential growth function, modifier function, and mortality function. The potential growth function estimates how rapidly trees would grow in d.b.h. if they did not interact with other stems. The modifier function reduces the potential change to correspond with observed data from permanent growth plots. The mortality rule computes a probability of death for a tree based on its species and growth rate.

Output from the model is a list of trees showing species, new d.b.h., and new status if the tree dies, plus associated product conversions and summary tables of stand characteristics. The projection system does not currently handle events such as ownership changes.

Prognosis.—In addition to STEMS, another individual-tree distance-independent model with potential for aggregate timber supply analyses is the Prognosis model for stand development (Stage 1973, 1979; Stage et al. 1980). This model has been extensively used in the northern Rocky Mountains. It has been adapted to all major tree species found in Idaho for both even-aged and uneven-aged stands and may be applied to similar coniferous types found in the Pacific Northwest.

The Prognosis model predicts future development of stands through displays of long-range values of tree diameters, heights, crown ratios, tree species composition, and understory shrub composition and coverage. Like the STEMS model, Prognosis uses species-specific, internal growth equations to simulate the growth and yield of individual trees, which can then be extrapolated to a stand basis. As with most individual-tree models, it is not restricted to specific cover types; rather it is applicable to stands containing any mixture of species or age and size classes that grow as a community (Stage 1973). Additional capabilities include conversion of tree dimensions to conventional units of timber yield in total cubic and board feet, as well as information related to wildlife habitat changes, watershed protection, and recreational values that can be derived from the fundamental tree and shrub variables.

The Prognosis model consists of a set of computer programs for combining current silvicultural knowledge with past growth data to make a forecast of stand development reflecting the effects of thinning, fertilization, and regeneration harvests. This program is capable of making projections for a period as long as a full rotation.

Input to the Prognosis model consists of habitat type, shrub cover and height, and conifer stocking. Input tree lists are described by species, d.b.h., and crown ratio. Removal of individual trees from an inventory plot are used to reflect harvests. The model depicts tree growth through a collection of submodels representing growth of trees at different stages in their life cycle. These stages are as follows:

1. Regeneration establishment that follows seedlings through the first 10 years of growth.
2. Regeneration development that represents growth of established seedlings and saplings up to the time they reach 5 inches d.b.h.
3. Poles and larger trees.

The regeneration establishment submodel predicts the stocking characteristics of small (1/300 acre) plots. This modeling of stocking rate requires inputs describing habitat type, slope, aspect, elevation, topographic position, time since disturbance, site preparation method, overstory composition and density, planting, and distance from seed source.

The regeneration development submodel predicts height and diameter increments of trees less than 5 inches d.b.h. Height increment is modeled using the height and species of the subject tree, overstory density,

conifer and shrub competition, habitat type, slope, aspect, and elevation. The diameter increment is a function of species height and predicted height increment.

The growth of pole and larger trees is represented by a set of species-specific equations that predict diameter increments from values of diameter, crown ratio, crown competition factor, basal area in trees larger than the subject tree, slope, aspect, elevation, habitat type, and geographic region. The height increments of these trees are dependent on predicted diameter increment, height, diameter, and habitat type.

The Prognosis model specifies mortality as a function of species d.b.h. and stand density (Hamilton and Edwards 1976). As with the growth functions, these relationships should be based on data from the area to which the model is to be applied.

Output from the Prognosis model is separated into individual tree summaries and forest stand summaries. Individual tree records consist of species, d.b.h., crown ratio, past diameter growth, and trees per acre associated with each of the original sample tree records. Forest stand records consist of numbers of trees per acre, distribution of d.b.h., volume characteristics of the total stand in cubic feet, surface areas of boles in square feet, and accumulated tree height. In addition, total cubic foot volume representing the growth of the initial tree population and the total cubic foot volume representing mortality are summarized (Stage 1973).

The Prognosis model has the capability to represent effects of pest populations (e.g., Douglas-fir tussock moth) on growth and mortality (Crookston 1978, Monserud 1978, Monserud and Crookston 1982). It may also be utilized to resolve discrepancies between inventory growth rates and model-based estimates, and to rescale model-based growth and mortality rates to represent nonmodeled silvicultural treatments such as fertilization or reduction in shrub competition. A parallel-stand growth processor permits interstand effects such as harvest allocation or pest contagion to be represented.⁹

Distance-Dependent Models.—The second type of individual-tree model requires intertree distances as a necessary input. Some representative distance-dependent models have been developed by Newnham (1964), Mitchell (1969), Arney (1974), Ek and Monserud (1974), and Daniels and Burkhardt (1975).

In these models, "individual trees" on a plot are assigned certain initial size and spatial distributions. The trees are then "grown" according to some function of their size, site, competitive status, and sometimes a random component representing microsite and/or genetic variability. Competitive status for each tree is quantified in terms of a competition index that is a function of the tree's size and the distance to and size of its neighbors. Mortality is regulated as a function of competition index, tree size, and/or growth. Yield estimates are made by applying volume equations to the dimensions of the trees (Curtis 1972), as in other individual-tree models.

Individual-tree distance-dependent models may provide more detailed stand and tree measurements than distance-independent ones. Several disadvantages of this type of model are that they require (1) intertree

distances as an input (this is usually not collected as inventory information), (2) a meaningful competition index for individual trees, and (3) more computing time.

Individual-tree distance-dependent models can be considerably more sensitive to harvest treatments and reproduction response than diameter class models (Ek and Monserud 1979). However, Ek and Monserud also suggest that whole stand models may project aggregate stand characteristics almost as well as individual-tree distance-dependent models at a much lower cost, within the range of data used to construct the former. Because of their detail and flexibility, individual-tree distance-dependent models may be most useful in analyses of optimal silvicultural alternatives (Adams and Ek 1974).

Although the growth and yield estimates are considered to be fairly accurate, currently the greatest obstacle to the use of these models for state and regional analyses are the data requirements for intertree distance coordinates and the expense of the required computer time. Another disadvantage is their use of stochastic methods for deducting mortality.⁹ As a consequence, the outcome of the simulation is itself a random process that should be replicated to estimate the expected value. For long-term projections or for high mortality, the variance of the output depends on the initial numbers of tree-records in the simulation.

PTAEDA.—The model PTAEDA, developed by Daniels and Burkhardt (1975), is representative of the single-tree distance-dependent models. PTAEDA simulates the growth of loblolly pine under a wide range of management alternatives.

The two major subsystems in PTAEDA deal with the generation of an initial precompetitive stand and the growth and dynamics of that stand. After PTAEDA was developed for old-field stands, management subroutines for unmanaged plantations were developed to simulate the effects of site preparation, fertilization, and thinning (Daniels and Burkhardt 1975). Trees are "grown" annually according to their size, site quality, and intertree competition. The probability of survival for each tree is calculated from a function relating each tree's individual vigor and its competitive stress as measured by estimates of photosynthetic potential. This probability is used to stochastically determine annual mortality.

Effects of certain management practices are incorporated into PTAEDA by modifying the original growth function. The efficiency of a site-preparation program is expressed as the degree to which a cutover site approaches old-field conditions. Growth reductions on cutover land are assumed to be solely due to competing vegetation, because degradation in site quality caused by past management practices could be described by initially specifying a lower site index (Daniels and Burkhardt 1975).

Similarly, the response to fertilizer treatments could be described as an increase in site quality, as suggested by Ek and Monserud (1974) and Hegyi (1974). For this reason, a site adjustment factor that acts as a multiplier for site index for fertilized stands is built into the model.

Intermediate thinnings result in a decrease in competitive stress for the remaining trees. These trees become more capable of competing for the limited

resources such as light, water, nutrients, or growing space. The response to these thinnings is moderated by a tree's own potential for growth as measured by a function of crown size (Daniels and Burkhart 1975).

Estimates of basal area per acre, trees per acre, total stem cubic foot volume, and total aboveground biomass are also given by PTAEDA. To further describe stand conditions, the output summary includes the mean, standard deviation, and range of relevant tree dimensions; the stand diameter distribution; the average height of each diameter class for live trees; the trees removed in thinning; and the trees lost to mortality. Farrar (1979a) indicates predicted yields agree with published reports for thinned and unthinned old-field plantations.

SUMMARY

Direct inventory projection methods have been used in most large-scale timber supply analyses. The utility of the TRAS model (Larson and Goforth 1970, 1974) has been demonstrated in the last several USDA Forest Service timber assessments. Although TRAS is fairly inexpensive to run, can represent any geographical level by the use of "average" acres, and has a projection system with fairly simple mechanics, it has been criticized in several respects. A major criticism is that TRAS is not very tractable as a tool for simulating changes in timber management intensities.

Among indirect methods for inventory projection, individual-tree distance-independent models have often been proposed as a replacement for TRAS. These models have the capacity to efficiently simulate silvicultural operations as well as to provide regional growth and yield projections. Models of this type that have proven most useful are the STEMS model (USDA Forest Service 1979) and the Prognosis model (Stage 1973).

The individual-tree distance-dependent models are capable of providing accurate growth and yield projections as well as detailed information about stand structure (e.g., Daniels and Burkhart 1975). Conversely, the large data requirements of intertree coordinates and excessive computer time have thus far prohibited use of these models for large-scale analyses.

Although the "inventory projection" models discussed were designed for somewhat different purposes, various opportunities exist for linking them in regional or national timber supply studies. For example, individual-tree-based models, such as STEMS, may be more precisely classified as variable density growth and yield able generators. They could provide "harvest scheduling" models with the necessary timber growth information to help drive an overall timber inventory projection system. Expanded and improved regional growth and yield modeling by such techniques will depend largely on progress in assembling growth and yield data in a consistent manner for all regions, which would facilitate modeling of alternative timber management possibilities. In particular, it is important that growth and yield model output forms be similar.

3. HARVEST FLOWS

Harvest flows represent the timber volumes removed over time from existing timber inventories or stock supplies of stumpage. The modeling of these flows is the central concern of aggregate timber supply studies. Linkages among harvest flows and the two components of aggregate timber supply analysis discussed previously—land allocation and timber growth and yield—involve dynamic interrelationships between biological and economic forces. Furthermore, because timber inventory is both invested capital and product, modeling of harvest flows is also conceptually linked to timber investment processes that impact future inventories from which harvests will be drawn.

This intertemporal linkage of harvest decisions and longer term investment decisions may involve adjustments in timber inventory structure and volumes to achieve long-term objectives, such as profit maximization, with investments (e.g., fertilization) or disinvestments (e.g., harvest) based strongly on future expectations of the timber economy. Timber market fluctuations in the short term may prompt previously unforeseen revisions of long-term adjustment paths so that short-term gains may be realized. Navon (1982) observes that the time path of aggregate harvest responds to market conditions when present net worth is maximized, as would be the case with industrial and some nonindustrial private ownerships. For public agencies, however, this path is manipulated to provide a stable supply of timber and/or other socially dictated objectives.

Thus, the timing and intensity of harvests chosen by an owner are major decisions in long-run timber management strategies, and their estimation greatly influences the projected results of other analytical components in timber supply studies. In theory, harvest patterns would be chosen to maximize discounted economic returns over an infinite time horizon, if the owner's goal were profit maximization. However, the planning horizons which underlie actual harvest decisions vary greatly among owners with respect to short-run versus long-run perspectives. These differences can be attributed primarily to varying financial flow needs and uncertainty regarding financial returns from various forest management strategies.

While marked differences among harvest patterns and length of planning horizons exist for the numerous types of forest land owners, the flexibility in timber resource adjustment and harvest over time is constrained to a large degree by underlying biological and economic processes of timber production. Distinguishing between short-run and long-run situations in aggregate timber supply analysis is somewhat problematic, especially in view of the long production periods inherent in timber production. In an economic context, the short run is characterized by the presence of a fixed production factor, while in the long run all factors are considered variable. Lyon and Sedjo (1983) observe that in forestry the short run embodies a perspective of timber production in which timber manifests many characteristics of a nonrenewable resource. In this context, the question of

short-run supply relates to the rate at which the existing stock is harvested.

Duerr (1960) also proposes temporal characterizations or conditions for timber supply: stock supply, short-run supply, and long-run supply. Stock supply of stumpage arises from existing timber inventory and, because the existing growing stock inventory is also the stumpage factory, stock-supply responses tend to overshadow the other two supply responses. Stock supply is theoretically governed by the opportunity costs of holding the stock or inventory in relation to alternative rates of return. Short-run supply depends upon the rate of growth of the growing stock and, consequently, upon the cost of variable inputs that might be used during a timber rotation. Land is the main fixed input, and the short run may consequently span several decades. The long run corresponds to the period when all inputs are variable, including the decision whether to invest in timberland.

Although this outline of Duerr's (1960) timber supply theory is somewhat simplified, it still suggests the complexity of the dynamics of timber supply over time. With aggregation across many timber management situations, including various forest stand structures and conditions and diverse ownership classes with varying time frames and differing management perspectives, it becomes exceedingly difficult to distinguish between short run and long run for analytical purposes. The criterion of land as a fixed factor of production over a particular time period may apply to some owners but not to others. Thus the precise time period for which this factor remains fixed may be difficult to identify from an aggregate standpoint. Aggregate analysis in effect synthesizes a broad range of rotations which vary according to a wide variety of species and management conditions.

The concept of the short run as the transition period, during which the gradual depletion of old-growth timber and the merging of various management patterns results in a "steady state" forest situation (Lyon and Sedjo 1983), represents one conceptual approach to this problem. In this context, the long run represents harvest levels after the steady state has been achieved. Such estimates are of obvious importance with respect to the long-term status of the timber resource; however, this framework is difficult to apply in empirical supply analyses. Such an approach is addressed further in the following section on timber investment modeling. The present focus is upon the major techniques for modeling harvest flows, with less emphasis placed upon explicit criteria for long-term investment strategies.

Modeling of aggregate harvest flows has generally been addressed through two distinct analytical approaches: (1) simulation of harvest flows based upon historical relationships among current period harvest, stumpage prices, and some proxy for the opportunity costs of holding timber inventory (Adams et al. 1982); or (2) optimization techniques such as mathematical programming that schedule harvest flows so as to result in the maximization of some ownership objective.

Simulation models predict or display the consequences of a selected range of management alterna-

tives; they generally provide information for selection of a desirable strategy by some method external to the simulation model. Duerr et al. (1975) classify optimization or "analytical" models as those that evaluate alternatives in order to find an optimum. The modifier "optimization" is used in place of Duerr et al.'s "analytical" to conform to popular usage of these terms in the literature.

Simulation techniques are often used in positive analyses, i.e., those in which responses of the timber resource to management in the future are projected as a likely continuation of response patterns that occurred in the past. Optimization techniques are generally associated with the normative modeling concept in which goals or objective functions with associated constraints are specified or prescribed. The distinction between simulation and optimization techniques is not always straightforward (Field 1978); some modeling approaches incorporate both as, for example, in the case of a mathematical programming technique utilized within the broader framework of a simulation model. Despite their simultaneous use for some modeling problems, simulation and optimization are discussed separately as the two most commonly used approaches for the modeling of harvest flows in aggregate timber supply analyses.

SIMULATION TECHNIQUES

Simulation has been used to represent the dynamic processes for a wide variety of situations in forest management (Bare 1971). In simulating large-scale forestry systems, key parameters and variables may be systematically varied to allow monitoring of system performance under a range of conditions. A dynamic simulation model is a representation of a system as it evolves over time. A deterministic simulation model does not contain variables, otherwise it is stochastic. Difficulties, inherent in model validation, including statistical validation problems for stochastic simulation models, are discussed by Reynolds et al. (1981).

With respect to the modeling of aggregate harvest flows, simulation techniques have employed various assumptions regarding harvest trajectories. For example, baseline simulations have been obtained by assuming that harvest levels would increase until they equal annual growth (USDA Forest Service 1973). While earlier simulation efforts tended to focus upon biological and/or silvicultural aspects of timber management, the emphasis in simulating harvest flows appears to be shifting more toward incorporation of economic variables or proxies (Adams 1977, McKillop 1967, Robinson 1974). Simulation of the response of private timber harvest to changes in production costs and prices was used in the 1980 RPA Assessment (Mills and Alig 1979, Adams and Haynes 1980). Prior to this harvest responses to economic variables had generally been determined in a judgmental fashion for major national timber assessments.

TAMM.—The Timber Assessment Market Model (TAMM), used in the 1980 RPA Assessment, is a compre-

hensive system of analytical techniques that models lumber, plywood, and stumpage markets in which supply and demand interact to determine equilibrium prices (Adams and Haynes 1980). Its stumpage supply modeling will be discussed as an example of simulating harvest flows using econometric techniques, which are statistical functions estimated by using economic precepts to guide model form.

TAMM's several analytical components estimate future prices, consumption, and production for softwood lumber and plywood, hardwood lumber, and both softwood and hardwood stumpage. Annual harvest flows are estimated by short-term supply functions, for which stumpage prices act as independent variables. These prices are obtained through a linkage of the stumpage and product markets; this is achieved by a complex simultaneous solution procedure for equations involving equilibrium prices and quantities (Adams and Haynes 1980). In effect, stumpage prices are estimated each model year for use in the short-run supply functions, and these supply functions shift over time as other independent variables change (e.g., timber inventory).

After the annual harvest flows are estimated in TAMM, they are then incorporated into the TRAS model (discussed previously) that has served as an inventory projection module for TAMM.¹⁰ The TRAS model then calculates the timber inventory progression for the next annual cycle. The timber inventory at the end of that simulated cycle is then fed into the short-term supply functions as one determinant of the next year's harvest volumes. This cycle then repeats over the time period of analysis.

TAMM is one of the most comprehensive models available for projecting timber market activities, partly because of the attention given to the spatial juxtaposition of the various supply and demand regions and the linkage of the stumpage and product markets. Regional competitive advantages attributable to differences across supply regions in the cost of timber production are an example of economic behavior that can be simulated by such spatial modeling. Also, stumpage prices computed by a simple simultaneous equations procedure using the equilibrium values from the product market are used in the stumpage supply functions to estimate harvest volumes.

Domestic supply region boundaries used in TAMM modeling for the 1980 RPA Assessment (fig. 2) were largely dictated by availability of aggregate forest inventory data (Adams and Haynes 1980). Short-run supply or harvest functions used in the 1980 RPA Assessment were estimated for the eight domestic supply regions separately for softwood and hardwoods and four ownership categories. For example, eight supply functions were estimated for softwood and hardwood stumpage supplies of four owner classes in the South-Central region, one of the domestic supply regions.

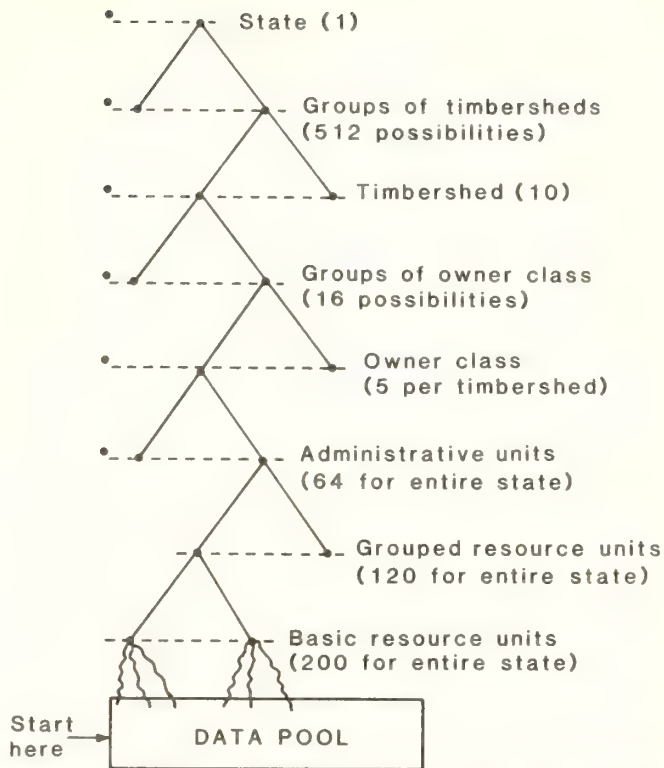


Figure 2.—Domestic timber supply regions used in the 1982 RPA Assessment (USDA Forest Service 1982).

The TAMM system has the flexibility for harvest flow estimations for more disaggregated supply regions, the major limitation being the existing levels of statistical reliability for collection and organization of data on timber inventories and owner supply behavior. This data limitation varies for different geographical areas, and augmenting data sources tends to be a long-term undertaking.

A typical (50-year) TAMM projection is relatively inexpensive because of TAMM's computerized nature, especially given the relatively low cost of long-term projections by the TRAS inventory projection module. The speed and low cost of TAMM projections make the system especially useful for sensitivity analyses. The influence of underlying assumptions can be tested through several projections by systematically varying input related to those assumptions.

The short-term harvest model embodied in TAMM is based on the following precepts: (1) private stumpage owners will vary harvest directly with stumpage price, and (2) private harvest will increase with available timber inventory levels (Adams and Haynes 1980). Adams and Haynes (1980) reported that TAMM explained historical harvest flow behavior reasonably well for the forest industry ownership in 1980 RPA Assessment analyses, but was generally not as successful in modeling private, nonindustrial harvest flows. TAMM's modeling of public stumpage supply behavior involves exogenously determined upper harvest bounds arising from allowable cut levels, established by legislated policies.

The modeling of private timber harvest by TAMM employs essentially the same functional forms for both

¹⁰The TRAS model itself has been modified to estimate harvest flows via stumpage-supply equations (Alig et al. 1982). Up to six independent variables can be specified for the equations (e.g., stumpage price) with the user providing both the appropriate variables and coefficients.

the industrial and nonindustrial owners. The relatively limited success in modeling nonindustrial timber harvest may be attributable to this parallel approach, which does not directly recognize the importance of non-monetary forest returns to nonindustrial owners. Also, industry-related considerations, such as aspects of integration in industrial firms, are ignored by TAMM's short-term harvest modeling, which is based directly on price and timber inventory variables.

TAMM's difficulties in successfully modeling harvest behavior of the diverse class of nonindustrial, private landowners have been preceded by numerous studies that suggest few generalizations can be made regarding timber management patterns by nonindustrial landowners (e.g., Stoddard 1961, Sizemore 1973, McComb 1975, Clawson 1979). Binkley (1979, 1981) has proposed a model of timber harvest behavior of nonindustrial, private landowners that addresses multiple objectives of ownership, in the context of balancing harvest income and personal consumption of the forest's nontimber outputs. Binkley's theoretical model is based on utility maximization through consumption of (1) goods and services purchased through income from timber harvests and (2) goods based on nontimber outputs from the forest (e.g., recreation).

Data was not available for estimating the theoretical timber supply model outlined by Binkley (1981). For example, existing data for even the relatively small study area was inadequate for estimating technical tradeoffs between timber and nontimber outputs. A "stochastic utility" model of choice was developed using the available data, with a maximum likelihood logit estimator used to estimate the probability of harvest. Because probability of harvest was analyzed and other study conditions were variable, Binkley's (1981) empirical results cannot be directly compared to those for TAMM's modeling of private harvest behavior. However, results of Binkley's work indicate that probability of timber harvest is strongly influenced by stumpage price, while income is negatively related to harvest probability. Farmers are shown to be more likely to harvest timber than nonfarmers, and the farmer group also appears to be more price responsive.

OPTIMIZATION TECHNIQUES

Optimization models represent another class of quantitative analytical techniques frequently applied to the modeling of harvest flows. While simulation procedures are often used to develop a range of alternatives without specifying a single most desirable solution to the modeling problem, optimization techniques are designed to identify a particular "optimal" solution that satisfies a set of predetermined output criteria.

The specific aim of optimization is the maximization (or minimization) of the value of an objective function that incorporates the goal of the modeling effort (e.g., maximizing present net value or minimizing costs). For some problems, the model is allowed to arrive at an optimal solution in an unconstrained fashion; in many instances, however, a variety of constraints are specified

as conditions for achievement of the optimal solution. Optimization models for timber management have generally been of this latter variety. Variables in the objective function and constraint equations, whose value in the optimal solution are to be determined, are referred to as decision variables.

Optimization techniques applied to estimate harvest flows in timber supply analyses have used a variety of biological, economic, and other specified objective function criteria, as well as a wide range of model constraints (e.g., Navon 1971). Johnson and Scheurman (1977), Bell (1977), Field (1978), Marty (1979), and Hann and Brodie (1980) review optimization tools for harvest estimation in even-aged forests, and Hann and Bare (1979) discuss techniques for uneven-aged cases. Optimization techniques evaluate harvest decisions as part of a total timber management package that includes other management practices; these management alternatives are prespecified external to the model. This important interdependency of the management variables in terms of joint optimization will be discussed further in the following section.

Among these optimization approaches, linear programming (LP) has been utilized most frequently for the modeling of harvest flows. This in part reflects the ability of LP to address large-scale modeling problems and its degree of computational efficiency relative to other optimization procedures. A primary assumption of any LP analysis is that the problem being modeled is capable of being formulated in such a way that an optimal solution to that problem may be found. A recent application of LP utilized by the USDA Forest Service for National Forest lands is discussed below as an example of the optimization framework for modeling harvest flows.

FORPLAN.—The Forest Planning (FORPLAN) model is a linear programming (LP) package that has been applied to the complex optimization problems associated with National Forest planning mandated by the National Forest Management Act of 1976 (Johnson et al. 1980). FORPLAN is actually a software package that serves as a linear programming matrix generator, an interface to the UNIVAC 1100 FMPS LP solution algorithm, and a report writer for describing the LP solution. The LP matrix generator converts data input into a matrix of rows and columns. This matrix is then used in the simultaneous solution of land allocation, land management or investment scheduling activities, and output mix. The report writer can produce final output in a variety of specified formats. FORPLAN essentially evolved from a timber management model known as the Multiple Use-Sustained Yield Calculator (MUSYC) and retains emphasis on timber analysis capabilities; however, prescriptions and output scheduling for a variety of resources can be examined as well, if relevant biological and economic information is available.

FORPLAN can construct an LP based on either Model I or Model II structures for timber harvest analysis (Johnson and Schuerman 1977). Basically, these two model structures differ in the manner in which they define timber management variables and handle multiple harvests within the planning horizon. In the Model

structure, a variety of management activities can occur on a particular land area over the entire planning horizon, with the specified area retaining its identity throughout the process. In the Model II approach, individual parcels of land are not kept intact through time because harvested acres are recombined into new management units. Model I is more effective in keeping track of location on the ground, while Model II is more conducive to minimizing model size. In terms of earlier timber management models, FORPLAN can employ the Model I structure of the Timber Resources Allocation Model (Timber RAM) developed by Navon (1971) or the Model II structure of the MUSYC model noted above.

Joyce et al. (1983) review the history and foundations of linear programming applications in the natural resources area, including the use of FORPLAN as a multiresource analysis tool for relatively small areas. The timber harvest analysis capabilities of FORPLAN are similar to other LP models used for optimization analyses (e.g., Ware and Clutter 1971), and they are discussed only briefly in this report. Johnson and Schuerman (1977) compare different types of LP models that utilize Model I or Model II frameworks, discuss the different solution techniques that have been applied, and also review quadratic versions of Model I and Model II (e.g., Walker 1971).

Basically, an LP model such as FORPLAN can maximize or minimize a linear objective function subject to linear constraints. Ten different possible forms of objective functions for FORPLAN are listed by Joyce et al. (1983). FORPLAN can also generate a piecewise approximated downward-sloping demand curve for timber. Fixed prices are assumed for all other outputs. At this time, costs can be assigned per acre for timber-related management prescriptions, and per unit output for all outputs (including timber). It is anticipated that the capability to assign costs per acre for all management prescriptions will soon be available in FORPLAN. An option to include fixed costs is also available in the model.

Output constraints or output targets are an important part of the LP formulation within FORPLAN. These targets set minimum or maximum levels of outputs to be obtained in the LP solution and actually drive the model in some instances. Inclusion of certain specific targets is directly mandated by the NFMA regulations. The fifteen kinds of tables and graphs which constitute the outputs of the FORPLAN model include the objective function value, constraint output, land allocation areas, harvest reports (area and volume), economic reports (costs, prices, revenues, present net worth, present net benefit), regeneration levels, and cultural treatments (Johnson et al. 1980).

FORPLAN allows considerable flexibility in the user designation of analysis areas and management prescriptions. Analysis areas are assumed to respond the same way to a given management prescription, regardless of where they occur. Analysis areas are defined by six levels of identification: levels 1-3, user-specified land characteristics (60 categories for each level); level 4, working groups (9 categories); level 5, land classes (15 categories); level 6, existing vegetation classes (60

categories). Every alternative management prescription specified in FORPLAN must apply to a given analysis area. In addition, alternative prescriptions can be included to apply to the regeneration classes created by prescriptions with harvest practices.

Production coefficients associated with specific treatments and land types are input into the model as yield tables. They generally represent the number of units per acre of output resulting from a given treatment applied to a given analysis area. Prices and costs are entered in the same manner as the yield tables noted above. The time frame that applies to management prescriptions as well as to resultant outputs is quite variable; it may consist of up to 30 time periods of from 1 to 20 years each.

FORPLAN model formulations may involve constraints relating to any or all of the following: area and volume control, harvest flow (e.g., nondeclining yield), ending inventory, management emphasis and intensity, and cultural treatments. These constraints may be represented by numerous configurations, and generalizations are inappropriate in this report. For example, the determination of which management alternative to examine within the FORPLAN model, and the derivation of the associated biological response (e.g., yield tables) are for the most part forest-specific.

Apple (1982) surveyed FORPLAN users in 7 of the 9 USDA Forest Service regions regarding the utility of FORPLAN for planning activities on National Forest lands. Most respondents, who consisted primarily of forest planners and operations research analysts, indicated that between one and twelve initial model runs were required to obtain a usable solution. Approximately 60% of respondents were utilizing Model I for analytical runs; the remaining 40% were employing Model II. Model I was regarded as less costly and easier to track, while Model II was considered to be better suited for forest management data and a more flexible analytical tool.

Among some of the unexpected benefits arising from the use of FORPLAN, planners and analysts felt that it provided a better evaluation of inventory, an increased understanding of the role of economics in forest management, better coordination of management functions, and a better overall understanding of the forest management system. Problems listed most frequently included the need for more direction in model use, the lack of or poor quality of input data, and lack of time for analysis, particularly with respect to the performance of sensitivity analysis for model results. Users indicated that the major areas of information needs included economic data and yield data for timber and other resources.

Although the FORPLAN model has primarily been applied at the individual National Forest level, the relationship of forest-level FORPLAN implementation, as well as other optimization techniques, to aggregate timber supply analysis is of major importance within the context of this report. Aggregate timber supply analysis for national assessments necessarily involves a critical linkage of potential harvest flows from public and private sources; however, these two sources are typically modeled with varying detail. Public timber harvest flows

in the most recent national timber assessment were essentially exogenous estimates, while private harvests were estimated using TAMM's simulation modeling. Questions have arisen regarding the possible expanded use of FORPLAN output from forest-level modeling for national assessments, or use of a modeling framework similar to FORPLAN's but at a broader regional level.

These concerns regarding the potential applicability of optimization techniques for modeling public harvest flows at aggregate levels (e.g., National Forest region) are also relevant to the modeling of aggregate private harvest flows in some regions. The multilevel or hierarchical decision problem of different planning levels (e.g., national, regional, and Forest/local) is difficult to solve because of the need to recognize (1) that variables under control of policy makers are distinct from those under control of the micro unit or behavioral decision maker and (2) conflicting objective functions may exist for different owners throughout the hierarchy (Candler et al. 1981). The goals of economic units can also often be stated more explicitly and unambiguously at the micro level than at the macro level. Specification of appropriate or realistic objective functions and constraints at aggregate levels for the various owner classes could be difficult tasks, particularly for the diverse nonindustrial class. Aggregation across such diverse owner and timber resource conditions may also lead to relatively large model size and cost if needed modeling detail is to be achieved (Ashton et al. 1980). Little has been reported in the literature regarding the feasibility of modeling aggregate timber harvest flows solely within an optimization framework; however, mathematical programming has been utilized in somewhat analogous roles to model agricultural supply activities (e.g., Meister and Nicol 1975).

Another potential difficulty with respect to expanded use of optimization modeling involves questions regarding computational efficiency that stem from the necessity of arriving at a single optimal level in order to satisfy the production of a desired output (e.g., timber). As an alternative to addressing the large computational requirements of the LP process, Hoganson (1981) describes a method whereby the LP problem is formulated as a simulation. This simulation model is driven by shadow prices (dual variables in an LP formulation) and the iterative process continues until harvest levels are driven to a level close to that specified in the regional LP problem. The technique has the potential for significant cost reductions in the analysis of large LP problems.

OTHER APPROACHES

Goal programming (GP) is a particular form of LP used to find a solution to a resource allocation problem involving several objectives, subject to a set of linear constraints. Depending on the type of formulation, all goals may be considered simultaneously in a composite (and single) objective function or sequentially in a series of objective functions (Bell 1976, Field 1978, Field et al. 1980). The choice variables are deviational ones—

showing overachievement or underachievement of the specified goal levels of output. As with FORPLAN, most GP models have been applied to relatively small areas. Schuler et al. (1977) suggest that the largest application problem involves determination of the technical coefficients (i.e., the amount of output that can be anticipated from a given input).

Another approach based on mathematical programming is Berck's (1979) empirically based model of long-run timber supply behavior. Berck tested the hypothesis that private owners cut their timber at a rate exceeding an optimal one based on alternative rates of returns. This analysis involved estimating the rate of time preference indicated by the interest or discount rate implied in historical management of Douglas-fir by private landowners, assuming they maximized present value of profits. Berck found that cutting rates for private landowners indicated they were discounting the future at a rate much lower than the rate of return available for other private investments and much lower than that proposed by Arrow (1976) as a social discount rate. Berck's assumption of rational price expectations by private landowners in order to maximize profits over a 175-year period implies knowledge and behavior that may not be representative of many private forest land owners. Non-timber benefits from the private forests were not included in this modeling of private forest owner behavior.

TREES.—An example of a comprehensive approach to modeling aggregate harvest flows is the Timber Resources Economic Estimation System (TREES) (Johnson et al. 1975, Tedder et al. 1980) model. This model contains a number of harvest estimation options, including variable harvest scheduling methods that use a multiple iteration binary search. The aggregation scheme of the TREES model is noteworthy for its sophistication and flexibility.

The TREES model was originally developed for a comprehensive study of future timber supply for the state of Oregon (Beuter et al. 1976). The model projects different harvest levels in response to varying assumptions about land use changes, growth rates, trends in silvicultural intensity, harvest control policies, and utilization efficiencies. TREES is capable of (1) projecting timber volumes resulting from either natural stand development or in response to specified treatment activities, (2) simulating harvests at numerous administrative levels, and (3) considering multiple stocking levels in inventory projections. The TREES model can also project timber inventories for both even-aged and uneven-aged forest structures. The key to these capabilities is the availability of yield tables. TREES does not provide such tables; it uses them to make timber inventory projections. Input to the TREES model includes base growth and yield information via growth functions, tables, or a combination of the two. These are keyed according to forest type, site, and acreage of each class by owner and administrative unit.

Seven harvest scheduling options allow the user to simulate harvest levels under current public and private management practices and to simulate new harvest schedules to evaluate policy alternatives. These harvest

schedules are developed through either single (fixed harvest schedule) or multiple (variable harvest schedule) iterative computer runs. The three fixed methods do not use an iterative search to find the harvest level, so no optimization occurs (Schmidt and Tedder 1980).

The three fixed methods can schedule harvest in accordance with the following rules:

1. Area control: Number of acres to be harvested is determined by dividing total available acres by a prespecified rotation length.
2. Percent of inventory: A proportion (fixed or variable) of the available inventory is to be harvested each period according to the harvest priority chosen (e.g., oldest age first).
3. Absolute amount: A specified timber volume, selected on the basis of the harvest priority rule, is to be harvested each period.

The four variable or multiple iteration procedures embody principles of several other harvest scheduling models. In development of these timber flows, a binary search technique estimates the following:

1. An even flow of timber volume sustainable over an entire specified projection interval, similar to the approach used in the SIMAC model (Sassaman et al. 1972). Alternatively, an even flow of timber volume is estimated for each harvest period within the projection interval. When this technique is used, the allowable cut is recalculated at the beginning of each harvest period throughout the entire projection period. This approach embodies the ideas of the SORAC model developed by Chappelle and Sassaman (1968).
2. An even-flow as in item 1, except that the variable of interest is a linear function of volume instead of volume itself. Such volume-dependent variables include employment or gross revenue.
3. Harvest rates based on the economic criterion of present net worth (PNW) in a constrained maximization framework. This approach is similar to the ECHO model proposed by Walker (1971), where the volume harvested is determined for a timberland owner facing a negatively sloping demand curve that reflects quantity and price interactions and market power.
4. Harvest schedules to maximize present net benefit (PNB), which is the net discounted difference between a measure of the consumer's "willingness to pay" and total cost. This harvest scheduling method is analogous to item 3, except that it maximizes PNB rather than PNW, and the former is relatively more difficult to estimate. The output projections are given by timbershed and decade for timber volume and growth, volume and value of harvests, volume and value by products, and payments in lieu of taxes.

One of the strengths of the TREES model is its elaborate control structure when it is used to aggregate the timber harvests. This control structure organizes resource units in such a way that the model can keep separate and monitor a large number of resource units

(fig. 3). The hierarchical aggregation scheme of TREES can currently aggregate information for up to eight different levels.

The basic resource unit for TREES is the smallest piece of land for which a beginning timber inventory may be entered. Examples of resource units from the Oregon study are even-aged units represented by volume per acre by age class, site class, and species for western Oregon, and uneven-aged units represented by number of trees per acre by diameter class in eastern Oregon. The next level of aggregation is the grouped resource unit, a collection of basic resource units all possessing a similar resource quality (e.g., a group of forest stands of single species and site class and all being managed under the same harvest method). The grouped resource units or management units are the lowest level at which timber harvests and projections are estimated.

Grouped resource units can be combined to form administrative units. Administrative units are sensitive to institutional constraints and closely follow the level at which federal harvests are regulated. Harvests are generally calculated at this level, and each projection has its own assumptions about land use changes, management intensities, and harvest control procedures.

Administrative units may be combined within an owner class, and owner classes can be grouped within a timbershed. The timbersheds can then be aggregated into groups within a state or a multistate region. For the Oregon study, the state was divided into a collection of timbersheds that were defined as the geographic area from which the primary needs of a wood processing center were supplied. A major advantage of the flexible aggregation scheme of the TREES model is that harvest quantities can be determined at any level from the grouped resource unit up to the state level.

The TREES model was also utilized in a Pacific Northwest Regional Commission Study of timber supply in Washington, Oregon, and Idaho (Rahm 1981). In the baseline analysis, the harvests of public sector owners are assumed to continue along the current planned path through the next century. Private timber owners are assumed to respond fully to market forces, harvesting timber at a rate that maximizes the present net value of their timber income stream in every decade for the next 100 years. In an "optimizing simulation," the TREES model selects harvest schedules in conjunction with downward-sloping demand curves (net of planned public harvest) for delivered logs in two subregions. The assumed objective function is the maximization of present net benefit; harvests are selected in each time period so that the discounted net revenue from the last (marginal) unit of wood harvested is just equal to what that unit would yield if allowed to grow and be harvested in the next time period.

Because the flow of delivered logs is the focus of this equilibrium analysis, the costs of removing and hauling the timber determine the corresponding stumpage sources. Per unit costs by age class for felling, bucking, skidding, and hauling are required for final harvests and thinnings. Price adjustment factors are utilized to

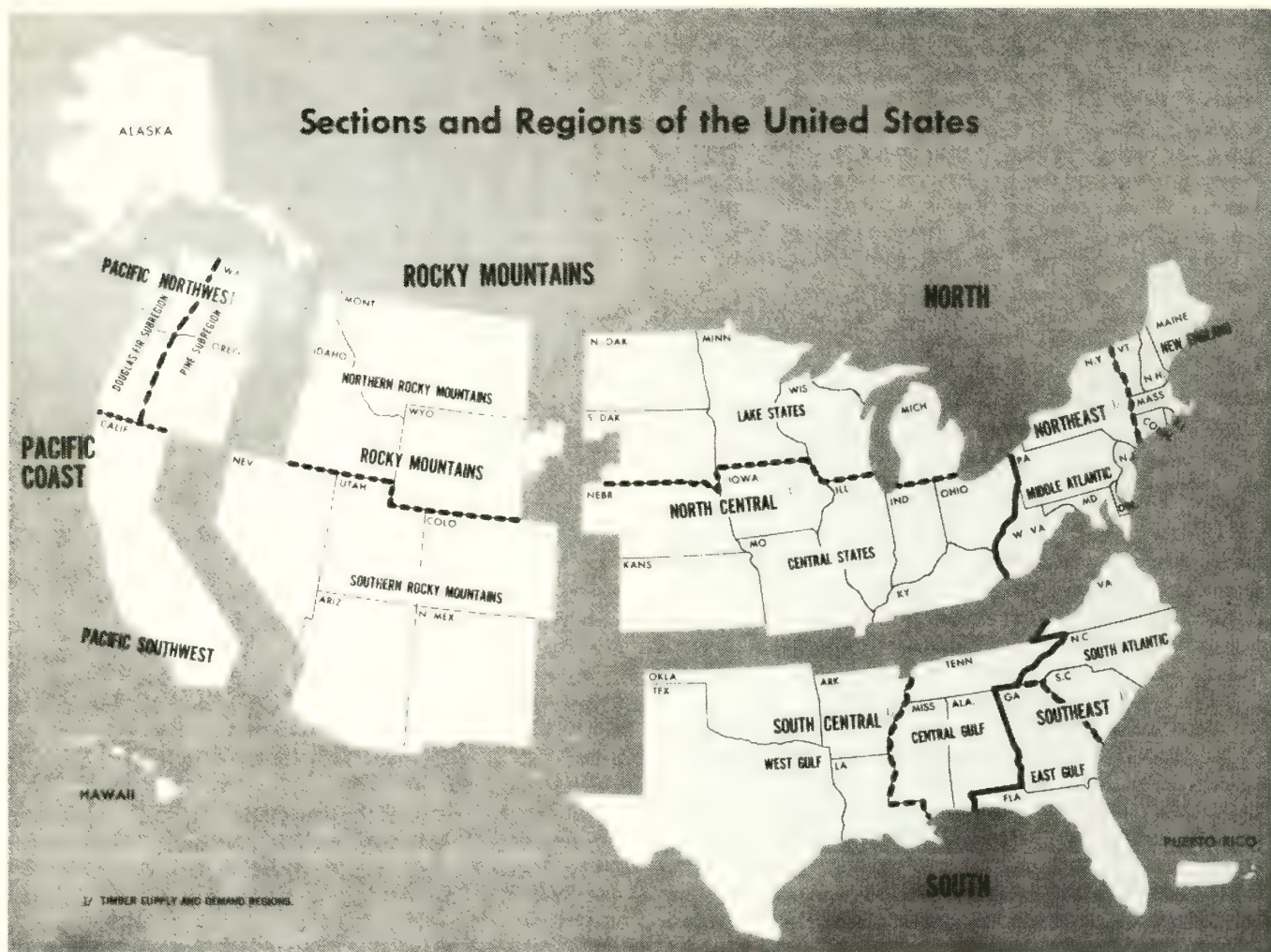


Figure 3.—Control structure of the TREES model used in Oregon study to aggregate timber supply information (adapted from Johnson et al. 1975).

reflect the differing values of logs harvested from stands of different ages.

Following this study, Rahm (1981) pointed out the following model limitations with regard to timber inventory projection capabilities of the TREES model: (a) certain combinations of timber management activities cannot be simulated, necessitating the use of broad average management practices; (b) the time path of changes in timber management intensity seems unrealistic because the proportion of total acres in a class rather than the proportion harvested is shifted after harvest; (c) a management intensity change (e.g., fertilization in middle-aged natural stands) cannot begin until acres are harvested; and (d) acres shifted from nontimber management to timber management are assumed to have the same average age structure and volume per acre as acres already in the management base.

While the TREES model considers the cost of removing timber from the stump and transporting it to market, Rahm (1981) indicates that the model does not properly specify the changes in costs associated with shifts in the geographic concentration of harvests over time. The model selects timber for harvest in areas that yield the

highest average net value based on the harvest costs. This constrains timber harvests solely to a subset of analysis areas (i.e., grouped resource units) in a stepwise manner, rather than having them more widely distributed geographically. Because of this intersubregional harvest optimization procedure, the resulting harvest flows may not necessarily be a realistic indicator of the actual location of future timber harvest within a region.

Rahm (1981) further points out that the TREES model tends to be expensive to operate because its "all purpose" orientation results in a size and complexity of the model that tend to make individual runs costly. Also because it is an extremely open-ended tool, a considerable amount of time is required for the user to become familiar with its operation. However, once basic model runs are set up, revisions can be made relatively quickly and large data sets can be accommodated satisfactorily.

The TREES model also does not necessarily calculate economic optima, but produces approximations because of assumptions such as those listed by Schmidt and Tedder (1980). For example, one assumption is equivalent to ignoring the opportunity cost of delaying future harvests.

Rahm (1981) suggests that such deviations from economic optima may not be significant in some applications, especially in view of the degree of error inherent in some data that is used.

INTEGRATION OF HARVEST FLOWS AND TIMBER INVENTORY PROJECTION MODELING

Linkage of the four analysis components in aggregate timber supply studies has been improved in recent years, particularly with respect to interactions between biological and economic processes. However, the modeling of harvest flows and investment has seldom been as detailed as that for timber growth in past studies. Future harvest patterns were sometimes estimated on the basis of simplified assumptions or scenarios, with no explicit consideration given to linkages with trends in important economic variables (e.g., prices). Despite recent efforts to devote more attention to economic processes, questions still remain regarding the appropriate balance of modeling detail for biological and economic components in aggregate timber supply studies.

While more effective integration of biological and economic models has slowly occurred, the flexibility of such analytical packages for examining timber supply policy questions is still rather limited. For example, the TAMM harvest flow modeling discussed previously relied on timber inventory projections by the TRAS model, which is relatively inflexible in its capabilities to simulate timber management alternatives. This rigidity in the biological simulation component diminishes the usefulness of the overall analytical package for timber supply analysis.

Models that are independently developed and later linked together often require major adjustments in order to permit efficient and effective joint operation. A major problem may occur when biological and economic models must interface at a common level of aggregation. For example, the integrity of TRAS's biological modeling may be diminished if it is applied to large geographical regions which serve as the bases for harvest flow equations or other economic modeling. Aggregation across many silvicultural conditions, such as site classes, stocking levels, and stand structures, may more adversely impact model validity for the biological modeling components than for those involved with modeling economic processes.

SUMMARY

The TAMM model (Adams and Haynes 1980) represents the most comprehensive approach for integrating short-run private harvest behavior based on historical patterns with long-term timber management strategies. Econometrically derived short-run harvest flow equations are shifted through time in a TAMM simulation, as in the 1980 RPA Assessment. Stumpage price and timber inventory levels are the independent variables in the harvest flow equations, which are somewhat ad hoc in

nature. The TAMM approach has the strongest explanatory power with regard to forest industry behavior, but it generally encounters major difficulties in attempting to explain the harvesting behavior of nonindustrial, private landowners. Other empirical studies of nonindustrial harvesting behavior include Binkley's (1981) dichotomous procedure for estimating the probability of harvest in a certain year. Although substantial data problems were encountered, stumpage prices were shown to strongly influence the probability of harvest.

The Forest Planning (FORPLAN) model (Johnson et al. 1980) represents the application of optimization techniques to the modeling of harvest flows. This linear programming (LP) model evolved from previous LP approaches for timber harvest scheduling, but FORPLAN differs from its predecessors in its multiresource dimensions. Applicability of the FORPLAN model and other optimization approaches to the modeling of aggregate harvest flows is hindered in part by difficulties in specifying objective functions and constraint equations for such analyses. Other mathematical programming approaches include Berck's (1979) empirically based model of long-term timber harvesting patterns. This modeling of the intertemporal dependency of harvest and management decisions involves estimation of private landowner rate-of-time preference as a behavioral parameter.

The Timber Resources Economic Estimation System (TREES) (Johnson et al. 1975, Tedder et al. 1980) is a relatively elaborate harvest scheduling model that has seven harvest scheduling options. The variable harvest scheduling methods (e.g., present net worth algorithm) use a multiple iteration binary search, and several options can be applied to either even-aged or uneven-aged stands. TREE's aggregation scheme has considerable potential for expanded adoption in aggregate timber supply studies, as it utilizes a comprehensive, hierarchical control structure. The aggregation control structure allows harvest quantities to be determined at any level from a grouping of basic resource units up to the state level.

4. TIMBER INVESTMENTS

Investments to enhance the productive capacity of forests involve utilization of inputs which influence the growth of the inventory over time and future harvest levels. The process of timber production may require input expenditures (e.g., artificial regeneration) well in advance of when the effects of those inputs are realized (i.e., gestation period). Capital theory deals with the time path of capital accumulation, and harvest flows discussed in the preceding section are part of the capital formation process in forestry, representing disinvestment or liquidation of accumulated timber capital stocks.

Although timber investments are important for long-run timber supply, analyses of aggregate timber investment patterns have been rather limited. Decisions to

undertake intertemporally linked timber investments such as planting, thinning, or fertilization theoretically depend on anticipated physical yields, opportunity costs of such investments, and stumpage prices. However, with the diversity of owner objectives (even within owner classes) and the widespread deficiencies in technical production and behavioral data, realistic modeling of long-term timber management behavior remains one of the more difficult tasks facing timber supply analysts.

The theory of aggregate forest investment is not well developed, and almost all applied timber investment analyses have been conducted at the stand level. While there has been considerable statistical testing of aggregate investment theories with regard to the general economy, results from these efforts have generally not been very satisfactory and no widely accepted theory of investment exists (Ackley 1978, Clark 1979).

Aggregate timber supply analyses have employed a variety of assumptions and approaches for modeling timber investment patterns in long-run supply studies. The importance of transitional, as opposed to steady-state, aspects of aggregate timber supply has been emphasized to different degrees in various studies of timber supply. Transitional patterns involve states of disequilibrium and change in the stumpage sector. The disequilibrium pertains to both stock variables that have no time dimension (e.g., timber inventory), flow variables (e.g., harvest) that are time dependent, and associated ratios of the two. Movements in the "system" comprising the timber economy may result in an essentially continual disequilibrium over time because of continuous changes in external circumstances such as productive techniques, population, consumer preferences, and government actions.

Conversely, some studies emphasize steady-state behavior for at least some aspects of a timber supply system over time. Examples are long-run harvest levels formulated according to constant economic parameters over time, or repetitive cycles of identical forest management strategies on land assumed to be initially bare. Steady-state conditions imply that relevant variables all grow at an identical rate, which is a generalization of the concept of the stationary state for which the relevant variables all remain constant (i.e., grow at a zero rate). The stationary equilibrium state is one in which the system operates in a similar manner year after year unless it is disturbed by some outside force. Furthermore, in steady-state analysis production functions or technology are assumed to be invariant over time. Some analyses may also assume asymptotic behavior in relation to inherent limits for the system.

The theory of long-term timber investment based primarily on steady-state or static profit maximization principles is discussed by Hyde (1980) and Jackson (1980). Hyde applies analytical tools based on economic efficiency norms in a Pacific Northwest timber supply analysis, and devotes special attention to public forest land activities. As previously mentioned, Hyde also gives an extended theoretical treatment of the economically efficient allocation of forest land among market and

nonmarket uses, which encapsulate long-term investment strategies.

Hyde's static approach focuses on the economic efficiency of public land allocation and management, and he concludes that increased levels of both timber and nontimber outputs are possible. This approach is similar to that of Clawson and Hyde (1976) and it does not address some timber market ramifications of increased public supply. These include the responses of private producers to any changes in public supply behavior and interregional linkages of product and stumpage markets. The important question in the Pacific Northwest with respect to old-growth timber and conversion policies is handled in a very general manner, with no examination of dynamic-adjustment paths. Feasibility of attaining a long-run annual harvest level that would not significantly increase relative stumpage prices is investigated, rather than the actual path of an optimal conversion policy and the resulting market implications.

Jackson (1980) orients his theoretical discussion toward the microeconomic framework of the private timber firm, developing a theory of timber supply under conditions in which production is time dependent. For example, under a particular set of assumptions, regeneration inputs and rotation ages as decision variables are shown to be substitutes, rather than complements, in the productive relationships. These types of timber production relations are important for long-term timber management analysis, and Jackson also points out information gaps that exist in the area of timber production processes.

Two different types of timber investment analysis techniques are discussed next which address dynamic aspects of long-term timber supplies—optimal control theory and analysis of investment opportunities in an overall simulation framework. These two analytical systems reflect a contrast between theoretical and applied timber investment modeling. They also focus on different aspects of the multidimensional timber supply question, particularly the distinction between short-term transitional supply responses and long-run stationary state behavior.

OPTIMAL CONTROL THEORY

Optimal control models describe the evolution of a system over time and determine optimal levels of decision variables over time, relying on the maximum principle of optimality (Clark 1976). State equations describe the evolution of the system from an initial state, resulting from the application of a given control. The fundamental problem in optimal control theory is to determine a feasible control that maximizes an objective functional (i.e., an optimal control) in order to determine an optimal path or trajectory through time. The maximum principle gives certain necessary conditions that must be satisfied by an optimal control. Techniques of optimal control theory can handle nonlinear optimization problems and inequality constraints.

SPOC.—The Supply Potential Optimal Control (SPOC) model is an optimal control theory model for estimating

regional long-term supply of timber (Lyon and Sedjo 1983). A recent application using hypothetical timber supply data addresses the constrained maximization problem of optimal timber harvesting and forest investments or management practices. A long-run supply potential based on economic considerations is investigated, using an endogenous determination of the economically optimal intertemporal levels of silvicultural inputs. Optimal rate of drawdown or conversion of existing old-growth stands is examined, and output levels are projected for steady-state conditions after the transition. Timber strategies that are examined pertain to the rate at which the timber stock is changed by rates of reforestation and afforestation, and also by other management that alters biological growth rates.

In the SPOC model, composition of the long-run supply curve changes as the transition progresses from short-run fixed timber stocks to those in the long run, where the stock is variable. Once the transition is complete, a steady-state forest situation ensues. The length of the transition period is specified beforehand, and the SPOC model does not solve for it using a simultaneous optimization approach.

Optimal long-term timber supply potential is analyzed by the SPOC model as a discrete optimal control theory problem, with the large multiperiod problem decomposed into a series of smaller, single time period problems. The model optimizes the level of management input and rotation length, and provides projections of regeneration, growth, and harvest for each class of forest lands. Important real world considerations such as ownership patterns and institutional constraints are considered to be noneconomic factors and are not addressed, given that the intent of the SPOC modeling is to focus on basic long-term biological and economic processes.

Biological variables are embodied in production functions in the SPOC model; initial conditions and "laws of motion" comprise necessary background information. Initial conditions include such items as acres of forest by age group and land class and composite regeneration input for each of the acres. Laws of motion are rules that govern the system, including those that redefine acres of trees in an age group and the regeneration input from one year to the next.

Economic optimization by the SPOC model proceeds by land class, with optimal regeneration input and rotation period calculated for the stationary state and then for the desired transition period. Control variables in the transition period phase are harvest levels and the level of regeneration input in each year by land class. The stationary state variables are the acres of trees by age and land class and the associated regeneration input for each of those acres. The model maximizes the discounted present value of the intertemporal net sum of producer and consumer surplus (net surplus) subject to an appropriate set of technological and cost constraints, with the optimal control theory algorithm used as the solution technique.

Optimal control variables are solved for by the use of gradient vector techniques, in which time paths are

based on the direction of maximum ascent of the present value of a "net surplus hill." Total costs are the sum of regeneration and harvesting costs. Regeneration input expenditures depend on the acres harvested, with no assumed regeneration lag. Harvesting involves a fixed entry cost per acre and a variable cost that depends upon total volume harvested.

Values for the objective function represent present value of the net surplus stream, which is maximized subject to a set of constraints. These are constraints on the values of the control variables and the laws of the motion of the system, e.g., the portion of acres harvested has to be nonnegative and less than or equal to one. Constrained maximization of the objective function proceeds by decomposing the overall problem into a series of subproblems (i.e., maximum principle). Each iteration in the gradient method moves the time path or trajectory of the variables closer to the optimum.

The gradient vector which determines the direction of maximum ascent of the net surplus hill is the derivative of the objective function with respect to the control variables. Thus, it is the vector of shadow prices or values of the control variables, i.e., rate of change in the objective function per unit change in a control variable. These shadow prices indicate whether an increase in a particular control variable will increase the value of the objective function.

Applications of the SPOC models have used hypothetical data to project the economically optimum time path of prices and harvest volumes. Variants of the model can be applied to examine regions where data are available; however, data availability in the short term may be a major constraint on actual application and testing of the embodied techniques. Lynn and Sedjo (1983) propose that several regions could be incorporated, if data were available, by introducing each region as a separate land class or groups of land classes.

The potential usefulness of optimal control models in aggregate timber supply analyses is difficult to evaluate because it is a relatively new analytical tool. Zilberman (1982) suggests that optimal control analysis is a powerful tool which expands the range of issues that agricultural economists can deal with, as well as increasing their effectiveness. Wide-scale application of this approach may be impractical at present, however, because of the data requirements for solving dynamic optimization problems. Optimal control models with stochastic elements are much more complex than deterministic ones (e.g., Lyon and Sedjo 1983), including the most advanced technique, named adaptive control, that takes into account the expected gains from future learning in determining optimal control levels (Zilberman 1982).

RELATED APPROACHES

Cohan (1982) also utilized optimal control theory in constructing a detailed theoretical model of private sector forest management and timber supply. This long-run model determines optimal investments in timber man-

agement activities (e.g., fertilization), the timing and levels of harvest, and cost-minimizing harvest patterns. This dynamic model of forest management and timber supply is based on the assumption of profit maximizing behavior and is linked to a set of simpler models of mills, market interactions, and forest products demand. This network is designed to be a flexible system of market equilibrium models of the timber industry. This optimal control model has also not been applied extensively to date.

Mathematical programming techniques, including linear programming, goal programming, dynamic programming, integer and mixed integer programming, and quadratic programming, have also been used in timber investment analyses (Bare 1971, Martin and Sendak 1973). They are designed to select an optimal solution for a set of variables, often called activities. The optimal outcome is the numerical maximum or minimum of some specified performance criterion or objective function.

Dynamic programming (DP) has been used at the stand level to solve for the simultaneous determination of rotation and intermediate treatments in timber investment analyses. The DP algorithm requires discrete time and stocking interval specification, in contrast to the use of continuous time or removal variables in some optimal control theory formulations. DP and its applications to forestry are discussed by Schreuder (1968) and Brodie et al. (1978). One of the earliest reported applications for analyzing multistage, sequential decisionmaking regarding timber investment paths was that of Amidon and Akin (1968). This is essentially a recasting of Chapelle and Nelson's (1964) marginal analysis of optimal loblolly pine stocking levels at the stand level (based on an iterative computer program) into a dynamic programming mode. More recent applications of DP are discussed by Brodie et al. (1978), Brodie and Kao (1979), Kao and Brodie (1979), Martin and Ek (1981), and Riitters et al. (1982).

ANALYSIS OF INVESTMENT OPPORTUNITIES

TAMM.—The TAMM model (Adams and Haynes 1980) examined in the previous section represents the applied state of the art in aggregate timber investment modeling. TAMM embodies a unique interregional linkage among long-term management or investment modeling, short-term supply (harvest) estimation, and stumpage price determination. Investment modeling by TAMM is based on normative analyses that involve economic maximization calculations, but are later linked to positive harvest flows modeling. Application of TAMM timber-investment modeling in an aggregate timber-supply analysis is discussed by Adams et al. (1982).

The TAMM investment model is an iterative process that determines the level of timber investment based on present net worth calculations and the associated extent of growth augmentation in the TRAS timber inventory projection module (Adams et al. 1982). Stumpage price impacts of those added investments are then

simulated, with only a part of the eligible investments undertaken each year. A new stumpage price is then fed back to recalculate the level of timber investment and growth augmentation. This entire cycle is repeated until there is a sufficient convergence of stumpage price. Convergence of price implies that price expectations at time of investment are actually realized when the investment matures and the resulting stumpage increment is marketed (i.e., perfect price expectations).

Forest investments influence short-term supply relations in the TAMM model, changing future harvests and stumpage prices. Owners are assumed to recognize this interrelation between investments and future prices, including all future investments, under the assumption of perfect price expectations. Constraints on rates of investments are imposed by limited availability of capital, with economic gain from timber production assumed to be the sole objective of all owners.

Constant discount or interest rates are used in the timber investment analysis in TAMM to account for opportunity costs of investing in timber growing; however, forestry is the only major land use considered, and changing relative prices for products from other uses of the land are not considered. Timber growers are assumed to have perfect price expectations (i.e., expected prices are actually realized when investments mature several decades into the future) and to have the sole objective of maximizing their financial position. Timber production yields and returns are also usually modeled under certainty, with no explicit allowance for land use shifts or productivity setbacks.

Reasonableness of assumptions such as economic rationality and perfect price expectations by private owners are difficult to evaluate fully because of the data deficiencies surrounding actual private timber investment behavior. Assuming profit maximization as the sole objective of the selection and implementation of timber management practices on private lands ignores other owner objectives and concerns for amenity and other nonmarket forest outputs. The annual rate at which admissible investments are undertaken is arbitrary because little is known regarding actual financial and other constraints that influence private timber investment behavior.⁷

The TAMM investment analysis techniques were first employed in the 1980 RPA Assessment (USDA Forest Service 1982). The development of the SPATS model for the South has also expanded the analytical capability of the TAMM system in terms of examining the timber supply impacts from government expenditures to subsidize timber management on nonindustrial lands (Brooks 1983b). Continuing research on the TAMM analysis framework includes development of a Timber Resource Inventory Model (TRIM) for major timber supply regions that incorporates modeling of management intensification practices. The general format of the TRIM model is based on attributes of the aggregation structure of the TREES model (Tedder et al. 1980) discussed earlier and also on TAMM's investment modeling (Tedder 1983).

Modeling of management intensification for even-aged stands by the TRIM model relies on the yield table

projection approach. This age class approach, similar to that for the TREES model, allows the timber inventory to be segregated so that management practices can be tailored according to site, species, stocking levels, and age. This is more specific than the 1980 TAMM approach, which relied on an augmented TRAS model (Barber 1980), where all acres in an aggregate were assumed to receive the same basic package of management practices over time.

The economic process that drives the TRIM investment model is based on perfect price expectations, as in the 1980 TAMM approach. If the estimated rate of return is equal to or exceeds a specified alternative rate of return, investments are implemented on a perpetual rotation basis. Annual prices used in the calculations of soil expectation values are taken from the TAMM model, while costs will be obtained from regional studies (e.g., Rahm 1981 and Dutrow et al. 1982). This timber resources inventory projection model would make projections by ten-year intervals, while linked to the annual TAMM market model.

OTHER MODELING CONSIDERATIONS

Applications of techniques for analyzing timber investment strategies are numerous, and many variations have been applied to the broad range of timber species across the nation. A cross section of these timber investment analysis techniques are listed by region in appendix C, which also includes sources of cost information useful for investment analyses. These techniques have frequently been constructed to analyze stand level treatment possibilities, and they are typically designed for analyses at substate levels (e.g., Hepp 1982). Thus, analysis of the biological and economic characteristics of alternative timber management schemes at aggregate levels would probably require considerable adjustments in associated timber growth and yield modeling to better address the less detailed but more extensive data needs of aggregate analyses.

All of the major timber investment analysis techniques currently available are based on normative decision rules, which assume that owner objectives are generally based on maximization of economic gain from the timber resource alone. No positive aggregate timber investment model has been reported, and timber supply analysts face the question of how to represent adequately realistic future price expectations mechanisms and likely supply responses by stumpage producers. Because planned supply responses or investment decisions involve estimates of the future based on imperfect knowledge regarding stumpage prices, technology, yields, institutions, etc., those future estimates are subject to error. Those errors give rise to differences between planned and realized supply response (Jensen and Day 1961, Stone 1970), and little is known regarding the extent of this gap for timber investments. Most timber investment analyses utilized in examining future timber supply levels also usually assume that all timber investments actually implemented will be carried to maturity at a certain productive level.

This latter assumption may be too optimistic in some cases because of evidence of investment failures and land use changes cited in several studies.⁴ Studies of the retention and condition of timber investments initiated through public programs are listed in appendix D. In general, an inconsistent and rather meager information base exists to support the appropriate degrees of adjustment of physical and financial yields of timber investments to account for unforeseen productivity reductions and land use changes. This is particularly true for non-industrial, private timber investments, which often are managed by several different landowners over a maturation period that typically spans at least several decades.

The various approaches to modeling aggregate timber investment have generally been normative in nature. They have emphasized different biological and economic dimensions, especially as they relate to the dynamics of timber supply. Static optimization techniques have been utilized to investigate displacement from equilibrium positions based on competitive market conditions, specified constraints, and the objective of profit maximization, but the explicit time path of variable changes is not predicted. A hybrid framework that uses short-run, empirically derived harvest relations in conjunction with normative long-term timber investment modeling in a dynamic analysis supports the first-generation TAMM model.

The proliferation in the application of operations research techniques in forestry over the past several decades has also led to a large body of literature on timber investment analyses using mathematical programming models suited to electronic data processing (e.g., Brodie et al. 1978). The mathematical basis of optimization techniques necessarily implies abstract representations of biological and social systems, with approximations and simplifying assumptions generally required if the model is to be tractable. The proper criterion for judging whether the formulated model is then a valid representation is whether it predicts the relative effects of alternative courses of action with sufficient accuracy to permit a sound decision (Hillier and Lieberman 1980). Such determination is quite subjective with respect to timber investment because long maturation periods hinder timely objective validation (and consequent modification, if needed).

AGGREGATION AND UNCERTAINTY CONSIDERATIONS

Estimating the validity of aggregate models and the concurrent degree of uncertainty associated with aggregate timber supply studies is a major problem. The degree of uncertainty inherent in estimating future components of timber supply is strongly related to the aggregation schemes employed, which by their nature condense diverse and complex relationships into a relatively small number of essential characteristics. The broad geographical range of most aggregate analyses invariably includes diverse owner classes with differing

timber management motivations, institutional constraints, resource and market knowledge, etc. Not only does this imply that predicting future timber supply is difficult, but in many situations substantial uncertainty exists with regard to current areas, volumes, ecological capabilities, prices, etc. (Bentley 1981).

Aggregation and uncertainty in timber supply modeling are related in part to the quantity and quality of historical data available as a basis for projection. Data deficiencies vary with respect to biological and economic dimensions of timber supply modeling, and also within these two broad categories. The levels of timber growth and yield data have been augmented significantly during the last several decades; substantial problems remain, however, regarding the suitability of such data for purposes of modeling responses to an array of management treatments.

Availability and quality of data for economic characteristics of timber management is also highly variable; data are particularly deficient in certain areas. A comprehensive data base for modeling landowner response to alternative market conditions does not exist; therefore, consideration of the dynamic nature of human interactions with biological and economic systems in the real world is quite limited. These deficiencies have forced analysts to employ less data-demanding models, often limiting the expansion of analyses to adequately include other resource interactions and impeding the construction of timber supply analyses at less aggregated levels. Strategies for dealing with data limitations are offered by Rose et al. (1981), while Hamilton (1978) and Lewis and Ellefson (1983) discuss related aspects of required levels of precision with respect to information needs for forest management.

Even with ideal data sources, however, determination of the mode of data aggregation for regional and national timber supply studies would likely not involve a straightforward decision process. Appropriate geographic bases sometimes vary greatly for analyzing ecological, social, and economic concerns in supply studies that include multiresource and institutional considerations. Although aggregation patterns may have a substantial bearing on the quality of supply analysis results, a set of useful aggregation guidelines based on adequate quantitative considerations has not emerged. At least initially, aggregation schemes are dictated by the objectives of a given study, but the direction of later adjustments in response to data availability is often not predictable.

Teeguarden (1977), in discussing the complex of factors involved in aggregation considerations for RPA Assessments, suggests that relatively homogeneous ecosystems be the lowest level of analysis, with subsequent aggregation to regions and to the nation. Marty (1969) and Beuter (1979) have suggested the need for less aggregated geographic and ownership groupings than have been utilized in national timber appraisals. While other suggestions can be found in the literature, no complete set of readily transferable guidelines based on quantitative or economic principles is available to aid in devising aggregation schemes for timber supply studies.

The question of appropriate level of aggregation also needs to be examined regarding timber demand as well.

Two additional aspects of data aggregation that may cause problems in timber supply modeling pertain to nonlinear systems and variance of aggregates.⁹ In the first instance, aggregation can cause bias in systems that are nonlinear, particularly for systems with many step functions (e.g., decisions to harvest, depending on volume or costs). The second case pertains to whether a particular model adequately represents the effects of variance in aggregates. For systems with strong positive feedback, ignoring variance may introduce bias (e.g., ignoring the variability of growth rates from the mean for large, dominant trees may produce underestimation of growth).

Aggregate timber supply results are generally based on analytical techniques dependent upon a mixture of experimental and nonexperimental data sources, with little (if any) indication of the overall statistical reliability of the ultimate results. The manner in which such statistical problems might interact or even be compounded over relatively long timber supply projection periods has generally not been addressed. While the problem of combining techniques or data of varying statistical reliability is not unique to timber supply analyses, the particular mixture of specific data problems and long time periods involved in timber supply studies create some special statistical concerns. Propagation of error does appear to limit the usefulness of large, relatively complex models.

One general approach used to address these problems has been the use of sensitivity analyses, the testing of the influence of changes in input items or assumptions on model results. Sensitivity analyses are especially relevant for mathematical programming techniques that are widely used in forest land planning, given the long planning horizons and the assumption of certainty for model inputs.

Sensitivity analyses have been applied in various fashions for timber supply analyses. For example, Frayer and Jones (1970) use a Monte Carlo technique to investigate the effects of each input item on timber stand projection variability. Results indicate that sampling errors for growth, mortality, removal, and in-growth parameters largely determine projection variability. Goforth and Mills (1975) devised a technique to determine degree of data error required to influence the outcome of timber investment analyses.

One proposal for improving credibility of natural resource supply forecasts involves the comparison of a series of relatively short-term projections with one continuous projection.⁵ In this approach, reexamination (and readjustment if necessary) of assumptions and techniques are possible at each breakpoint. Another suggestion involves definition of a systematic procedure to ensure that each component of the projection process and the overall process itself is examined for validity by specialists other than the forecaster/analyst and the potential users.⁵

Reducing the degree of uncertainty in timber supply analyses, or at least not unduly obscuring it in describ-

ing results of such studies, is a primary consideration in devising aggregation schemes. Much has been written on the general topic of uncertainty associated with investment analyses and planning (e.g., Borch 1968, Arrow and Lind 1970), with applications to forest land use planning discussed by Dowdle (1962), Marty (1964), Thompson (1968), Teeguarden (1969), Lundgren and Thompson (1972), and Fight and Bell (1977), among others. As noted in the previous section, Hoganson (1981) offers a specific approach for addressing the problem of uncertainty and accountability in stand-level optimization (i.e., linear programming) modeling by reformulating the linear programming problem within a simulation framework. However, there appear to be no standard pathways to follow in evaluating and tempering aggregate forest investment analysis or supply projections with regard to uncertainty. Zones of uncertainty, usually expanding greatly with time, are sometimes assigned to forecasted estimates in timber supply studies. However, their estimation and use appear to be rather subjective in nature.

A relatively large degree of uncertainty in timber supply analyses is related to the estimation of future technological changes. This refers to both innovation and implementation of technologies across diverse owner settings. According to economic theory, production function frontiers are based on application of the most efficient technology, which therefore implies a fixed technology base over the production period; however, production processes that stretch over several decades at a minimum suggest that this assumption may not be valid. While many recognize that substitution of other inputs (e.g., genetically improved trees) for land in timber production will increase in the future, precise forecasts of the rate and actual composition of the technical change are difficult to obtain. Heady (1952) has outlined some basic principles to consider in attempting to approximate the direction of the impact of technical change; these are based on the nature of the technical change and demand-supply characteristics of products (Castle 1977).

Aggregate timber supply studies can provide critical clues to issues regarding natural resources availability, but often such studies are questioned because adequate measures of risk or uncertainty are not provided. Most aggregate studies have employed deterministic models that provide only a point estimate of the outcome for a specified set of assumptions and timber management strategies. This is again related in part to data problems. It is not uncommon for timber growth and yield projections to be published without any meaningful indication of changes in the level of reliability over the projection period.

In summary, given that substantial uncertainty and aggregation bias might be associated with aggregate timber supply studies, the degree of sophistication warranted in a study's framework and underlying modeling techniques is largely a judgmental matter. Standard statistical tests or other objective guidelines are very difficult to apply in a comprehensive manner, largely because of the quality and mixture of available data. A

key question in the planning stages of a timber supply study is whether the study approach is consistent and efficient in terms of the stated objective.⁶ However, currently there are difficulties in determining changes in the quality of projection results needed to improve decisionmaking to selected degrees. This has also impeded rigorous and objective evaluations of model adequacy.

OVERVIEW OF METHODOLOGY

Techniques and supporting data bases for analyzing aggregate timber supplies have evolved at different rates for the four major analytical components reviewed: forest land use allocation, growth and yield of the timber resource, removals or harvest, and timber investments over time. Aggregate timber supply analyses prior to 1970 typically depicted timber supplies in physical or biological dimensions, with relatively little analysis of their relationship to market forces. Applied analytical techniques have generally evolved, however, from relatively simple ratio and trend analyses to the use of complex econometric techniques in modeling the equilibrium of supply and demand.

The allocation of land to timber production has been exogenously determined in national timber assessments, with adjustments in a residual timberland base reflecting changes in higher valued land uses. Systematic methodologies for projecting timberland acreages have been based largely on economic optimization criteria (e.g., Hyde 1980), with notable exceptions being Markov land use simulation (e.g., Burnham 1973) and econometric approaches (e.g., White and Fleming 1980).

The accuracy of results from projecting timberland acreages with techniques that embody optimization criteria has not been satisfactory in some cases, especially with regard to nonindustrial, private lands. Simulation techniques applied in attempting to remedy this situation have also met with limited success, primarily because of land use data limitations. Documented information for historical timberland acreages is characterized by irregular time frames and nonstandard classification criteria among major data sources.

Assuming that a method for characterizing the forest resource has been selected and the resource has been stratified on the basis of such a characterization, timber inventory projection models are used to project representative units of each stratum (or the entire stratum) over time in timber supply analyses. For example, simultaneous growth and yield equations (e.g., Sullivan and Clutter 1972) can be utilized for stand-level projections for a given initial density, age, site, etc., stratum. In an alternative approach, the STEMS model (USDA Forest Service 1979) generates projections on an individual-tree basis for a particular stratum.

Given the diversity of species types and physical settings, timber inventory modeling has evolved according to two approaches: direct and indirect methods. Direct methods involve modeling growth and yield for forest areas using only sampling information for those areas

(i.e., applying sample data directly back to the population from which the sample was obtained). An example is a stand table projection technique such as the TRAS model, which applies rates of change (e.g., mortality rate) to a set of initial stand conditions (Alig et al. 1982). TRAS has been used in several regional and national timber supply appraisals, but its design makes it somewhat inflexible for modeling impacts of alternative timber management strategies.

Indirect timber inventory projection methods are applied to subject stands larger than those from which the original growth and yield data are obtained, and essentially involve a two-phase process. Whole stand yield tables (McArdle et al. 1961) and variable density growth and yield tables or models (Buckman 1962) comprise the two broad classes of indirect methods. Variable density growth and yield models may be used to generate yield tables, and there are three major classes of these variable density models: whole stand (Buckman 1962), size class and/or growth component (Moser 1974), and individual-tree simulation models (Stage 1973). The first two classes rely upon aggregate stand characteristics such as number of trees or basal area in modeling forest development. The more recently developed individual-tree simulation models describe stands on the basis of characteristics of individual trees.

Individual-tree models are classified according to whether or not they incorporate intertree distance within the projection framework. Intertree distance-independent models are represented by the STEMS model (USDA Forest Service 1979) and the Prognosis model (Stage 1973). These models do not consider spatial patterns or individual-tree locations. Consequently, they are operationally faster than distance-dependent models (e.g., Daniels and Burkhart 1975), presumably without a significant trade-off in terms of modeling precision for aggregate timber supply studies. Distance-dependent models can provide relatively detailed evaluations of timber management alternatives, but are relatively taxing in terms of data requirements and computer time.

The design and implementation of an inventory projection system that would improve upon current capabilities for aggregate timber supply analyses are buffeted by multifaceted considerations. Data availability, accuracy requirements, cost effectiveness, time and personnel constraints, and manageability are examples of interrelated (and often conflicting) considerations that are difficult to weigh because of quantification problems. While the growing sophistication of computer programming technology facilitates construction of individual models with larger storage and computation capabilities, the reliance upon a single model (e.g., TRAS) in future aggregate timber supply modeling may diminish as the state of the art evolves. It is unlikely that a single growth model could provide the most efficient growth estimates for all species and conditions. Also, the incorporation or adaptation of all of the component relationships needed to apply any one model to all species and conditions would likely be impeded by translation and data availability problems. Linkage of models,

or the aggregation of results from distinct models (using statistical reliability standards), appears to offer substantial promise, though coordination problems will likely be substantial.

Timber inventory projection models suitable for large-scale analyses have generally been developed separately from economic analysis techniques, the latter having been subsequently linked to them for the purpose of modeling the interrelationships between biological development of timberland and human intervention. This has somewhat hindered supply analysts from examining impacts arising from shifts in timber management intensity suggested by investment analyses.

Harvest flow models interface with timber inventory projection models in modeling the impacts on inventory development that result from adjusting timber inventory levels in response to harvest decisions. Harvest flows are often calculated as part of an overall, optimal, timber management package based upon long-run considerations (e.g., Hyde 1980). However, in the 1980 RPA Assessment, such harvest flows were modeled as short-run functions of stumpage price and timber inventory levels (Adams and Haynes 1980).

Simulation and optimization techniques have been utilized separately or in various mixtures in modeling aggregate harvest flows. These approaches differ with respect to the assumed basis of stumpage supply responses of producers, including the posited intertemporal linkage between harvests and long-range investments. The TAMM model (Adams and Haynes 1980) simulates future harvest flows by using econometrically estimated short-run equations based on observed values from a historical period approximately several decades in length. An optimization model such as FORPLAN (Johnson et al. 1980) seeks to maximize (or minimize) the value of an objective function that includes values for decision variables representing management practices for specific areas. Thus, simulation models have been employed to project timber supply trends based on historical patterns or other assumptions, while optimization models can estimate potential supply responses linked to efficient shifts in timber management on some lands (assuming certain goals). The basic distinction is between simulating how the system tends to operate, in contrast to how it could operate according to some norm or optimality rule.

Simulations of timber supply activities in aggregate timber supply studies have typically been made with econometric techniques, which use statistical methods to quantify economic relationships. Econometric models for aggregate timber supply processes often include several variables that are exogenous to the model, thus leading to a partially open modeling structure. In particular, macroeconomic variables (e.g., interest rates) may exert large influences on timber supply activities. These are quite difficult to forecast for future conditions, particularly when the long time horizons characteristic of forestry planning are considered. Other simulation techniques that might be used in place of or in conjunction with econometric techniques are stochastic simulation and system dynamics. In particular,

system dynamics may allow a more explicit method for modeling the complex interactions that characterize timber supply processes, while providing a general level of understanding regarding the associated dynamic tendencies over the long time periods (Meadows 1980).

While simulation models are readily adaptable to the modeling of aggregate harvest flows, optimization techniques such as linear programming encounter difficulties regarding specification of appropriate objective functions and constraint equations for regional or national analyses (McCarl and Spreen 1980). This problem is significant for both private and public ownerships. The extent of deviation of actual harvesting patterns from "optimal" timber harvest and management strategies assumed or portrayed in optimization analyses is presently unknown, but some evidence exists concerning management activities applied to cost-shared timber investments on nonindustrial private lands (e.g., Kurtz et al. 1980).

Modeling of aggregate timber investment behavior has been integrated with that for harvest flows in several different ways. An example of incorporating timber investment patterns based on optimization criteria within an overall timber supply simulation approach is the TAMM modeling applied for the 1980 RPA Assessment (Adams et al. 1982). A different approach is exemplified by the long-term timber supply potential model developed by Lyon and Sedjo (1983). This is based on optimal control theory and projects harvest and investment levels during both transitional and steady-state phases. Such an approach allows simultaneous determination of harvest and investment levels over an analysis period; it has not been extensively applied and tested to date.

The current array of timber investment analysis techniques at the stand level varies considerably across the country, primarily because the degree of sophistication of the underlying growth and yield modeling is not uniform across regions. Timber growth and yield characteristics differ so greatly across some geographical locations in terms of species, physiography, climate, and other factors, that separate growth and yield models must be linked to relatively standardized economic analysis tools for particular regions. As a consequence, differences in the evolution of data collection and biological response modeling efforts for various packages of timber management treatments have resulted in varying capabilities for evaluating timber investment opportunities in different parts of the country.

Specific areas of improvement needed in long-term timber management modeling include positive timber investment modeling and more in-depth examination of the dynamics of timber inventory development in response to varying degrees and timing of investments. At present, no positive models of aggregate timber investment behavior exist. Empirical work devoted to the statistical testing of timber investment theories has been quite limited, and no fully satisfactory or widely accepted theory of aggregate, long-term timber investment has been established. A better understanding of private timber investment decisionmaking is required, par-

ticularly with respect to the processes of economic expectation formation (e.g., as for stumpage prices) for conditions that may not actually materialize for several decades at a minimum. Appropriate levels of detail and abstraction for aggregate timber investment models also require careful scrutiny, including the establishment of useful measures of general aggregate investment behavior.

Investment modeling based on the assumption of timber profit maximization by owners may represent an upper limit or overestimation of actual investment, in light of the currently deficient data and analyses related to other objectives for various owner groups. From an overall perspective, generalizations regarding appropriate levels of abstraction and aggregation in aggregate timber supply studies are tenuous; this is due in part to the varying objectives of such studies and to difficulties in verifying whether harvest and investment patterns depicted by these models adequately reflect actual occurrences.

The degree and timing of future improvements in aggregate timber supply analysis may depend upon measures taken to strengthen existing data sources. Data deficiencies have been alluded to within numerous timber supply studies, which themselves have generally drawn on a variety of data sources. With respect to basic timber supply data, timber resource data is sometimes criticized as being inadequate for modeling purposes; however, economic data may be even less adequate. This has particularly hampered econometric analyses, which require reasonably long series of consistent price and production data. For example, data on timber production and transportation costs based on location and accessibility considerations have not been assembled or organized in readily retrievable forms for use in extending supply modeling capabilities.

The quality dimensions of timber supply represent another instance in which data deficiencies have impeded modeling. Timber supply at aggregate levels is comprised of many species, sizes, and grades of trees or logs, each of which may have a distinct price. Existing data do not presently allow these differences to be extracted or monitored.

Some of the primary improvements needed in aggregate timber supply data include:

1. Levels of private timber harvest by region and owner group.
2. Timber inventory by region and owner group.
3. Socioeconomic characteristics of forest owners (e.g., income)
4. Actual timber investment behavior by forest owners.
5. Forest land management opportunities by region and owner group (collected on a periodic basis).^a

The bulk of the empirical aggregate timber supply analyses can be described without reference to anything but the most basic microeconomic theory. While the transition from theoretical abstraction to empirical reality has been hindered by data problems, numerous opportunities exist to build upon basic timber supply

theory a structure that is more flexible and realistic with regard to the diverse ownership settings.

Ultimately, research may provide an overall model capable of representing aggregate timber supply according to the theory of the rational forest owner.⁸ This will entail the simultaneous determination of the levels of timber harvest, intensity of timber management, and land area devoted to the timber growing enterprise over time (along with supporting timber inventory projection capabilities). It will require more attention to the systems structure of the analytical problem (e.g., feedback loops and performance criteria) which in turn may provide a framework for integrating the components of aggregate timber supply analysis. An additional requirement is a better understanding of owner objectives, including the nature and extent of interest in market and nonmarket forest products and the "role" of the forest enterprise in the overall operations of a forest owner, as well as the role of forestry in local, regional, and national economies. However, given the state of the art and data deficiencies, analysts will be forced in the interim to separate the overall problem into smaller, more tractable components, as outlined in this report.

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Appendix A.—The date, primary analytical approach, and scope for major aggregate timber supply studies in the United States

Study	Year	Analytical approach	Scope
USDA Forest Service (Capper Report)	1920	Growth-drain ratio analysis	U.S.
USDA Forest Service (Copeland Report)	1933	Growth-drain ratio analysis	U.S.
USDA Forest Service (Reappraisal)	1948	Growth-drain ratio analysis	U.S.
USDA Forest Service (Timber Resources Review)	1958	Growth-drain ratio analysis	U.S.
USDA Forest Service (Timber Trends)	1965	Growth-drain ratio analysis	U.S.
Gedney et al. (PNW Economic Base Study)	1966	Stand table projection	Pacific Northwest, Inland Empire
USDA Forest Service (Douglas-Fir Supply Study)	1969	Investment analysis and even-flow modeling	National Forests in Douglas-fir region
Vaux	1970	Investment analysis and even-flow modeling	Douglas-fir region
U.S. President's Advisory Panel on Timber and the Environment	1973	TRAS stand table projection and supply/demand "gap" analysis	U.S.
USDA Forest Service (Outlook)	1973	TRAS stand table projection and supply/demand "gap" analysis	U.S.
Gedney et al.	1975	TRAS stand table projection	Pacific Coast States
Clawson and Hyde	1976	Yield-table projection with investment analysis	Coastal Pacific Northwest
USDA Forest Service (Assessment)	1976a	TRAS stand table projection and supply/demand "gap" analysis	U.S.
USDA Forest Service (Timber Harvest Scheduling Issues Study)	1976b	Investment analysis and even-flow modeling, with price projections	National Forests
Rahm	1981	TREES inventory projection, with economic simulation of timber harvests utilizing a downward sloping, regional demand	Washington, Oregon, Idaho
USDA Forest Service (Analysis of the Timber Situation)	1982	TAMM economic equilibrium modeling	U.S.
Brooks	1983b	Yield table projection, with investment functions and linkage to the TAMM model	Private lands in the South

Appendix B.—Selected recent studies of growth and yield modeling
identified by principal species and region

Author	Year	Principal species	Geographic area
Whole stand models			
Adams and Ek	1974, 1975	Northern hardwoods	Lake States
Alexander et al.	1975	Engelmann spruce	Colorado, Wyoming
Alig et al.	1982	U.S. species	U.S.
Alimi and Barrett	1977	Mixed conifer hardwood	Northeast
Barnes	1955	Slash pine	Florida
Beck and Della-Bianca	1970, 1972	Yellow poplar	Southern Appalachians
Bennett et al.	1959	Slash pine	Southeast
Bennett	1970a, 1970b	Slash pine	Southeast
Bennett and Clutter	1968	Slash pine	Southeast
Brodie and Rose	1975	Jack pine	Wisconsin
Bruce et al.	1977	Douglas-fir	Pacific Northwest
Buckman	1962	Red pine	Lake States
Buongiorno and Michie	1980	North Central hardwoods	North Central States
Burkhart et al.	1972a	Loblolly pine	Southeast
Burkhart et al.	1972b	Loblolly pine	Southeast
Burkhart and Strub	1974	Loblolly pine	Southeast
Cao et al.	1982	Loblolly pine	Southeast
Chambers and Wilson	1972	Douglas-fir	Pacific Northwest
Chambers and Wilson	1978	Western hemlock	Pacific Northwest
Clutter	1963	Loblolly pine	Southeast
Clutter and Allison	1974	Monterrey pine	New Zealand
Coile and Schumacher	1964	Loblolly and slash pine	South
Curtis	1967	Coastal Douglas-fir	Coastal Pacific Northwest
Curtis et al.	1981	Coastal Douglas-fir	Coastal Pacific Northwest
Dahms	1964, 1975	Lodgepole pine	Oregon
Dale	1972	Mixed oaks	Iowa, Missouri, Kentucky, Ohio
Dell et al.	1979	Slash pine	South
Dieraul and Mader	1965	Loblolly pine	Southeast
Edminster	1978	Ponderosa pine, lodgepole pine, spruce-fir	Rocky Mountains
Ek	1974	Northern hardwoods	Lake States
Ek and Brodie	1975	Aspen	Lake States

Appendix B.—Selected recent studies of growth and yield modeling
identified by principal species and region (continued)

Author	Year	Principal species	Geographic area
Farr	1967	White spruce	Interior of Alaska
Farrar	1979	Longleaf pine	South
Fedducia et al.	1979	Loblolly pine	South
Gardner et al.	1982	Mixed hardwoods	South
Goebel and Shipman	1969	Loblolly pine	South Carolina
Goebel et al.	1974	Loblolly pine	South Carolina
Gruschow and Evans	1959	Slash pine	Southeast
Hann	1980	Ponderosa pine	Southwest
Hoyer	1975	Douglas-fir	Pacific Northwest (Washington)
Lenhart	1972	Loblolly pine	Texas
Lenhart and Clutter	1971	Loblolly pine	Georgia
Lohrey and Bailey	1977	Longleaf pine	Louisiana and Texas
Lynch	1958	Ponderosa pine	Northeast Washington, Idaho, West Montana
Lynch	1982	Mixed species: aspen-white pine	Lake States
MacKinney et al.	1937	Loblolly pine	Southeast
McArdle et al.	1961	Coastal Douglas-fir	Western Oregon, Washington
Meyer	1938	Ponderosa pine	West
Moser et al.	1979	Mixed hardwoods	Lake States
Murphy	1982	Shortleaf pine	South (West Gulf)
Murphy and Sternitzke	1979	Loblolly pine	South (West Gulf)
Myers	1971	Ponderosa pine	Rocky Mountains
Myers et al.	1976	Ponderosa pine	Southwest
Nelson et al.	1961a	Virginia pine	Southeast
Nelson et al.	1961b	Loblolly pine	Southeast
Payandeh	1973	Northern species	Southeastern Canada
Schlaegel	1971	Aspen	North Central States
Schnur	1937	Oak-hickory	East
Schreuder et al.	1979	Slash pine	South
Schumacher and Coile	1960	Southern pines	Southeast
Smalley and Bailey	1974a	Loblolly pine	Southeast
Smalley and Bailey	1974b	Shortleaf pine	Southeast
Smith et al.	1975	Mixed hardwoods	South

Appendix B.—Selected recent studies of growth and yield modeling
identified by principal species and region (continued)

Author	Year	Principal species	Geographic area
Solomon	1977a, 1977b	Northern hardwoods	New England
Staebler	1955	Coastal Douglas-fir	Western Oregon, Washington
Sullivan and Clutter	1972	Loblolly pine	South
USDA Forest Service	1976c	Southern pines	South
Warrack	1959	Douglas-fir	British Columbia
Wiley and Murray	1974	Coastal Douglas-fir	Pacific Northwest
Worthington et al.	1960	Red alder	Pacific Northwest
<u>Individual-tree distance-independent models</u>			
Botkin et al.	1972	Northeast mixed forest	Northeast
Ek et al.	1980	Pure or mixed species stands	Lake States
Goulding	1972	Douglas-fir	British Columbia
Lemmon and Schumacher	1962, 1963	Ponderosa pine	Rocky Mountain Region
Martin	1978	Red pine	Wisconsin
Oliver and Powers	1978	Ponderosa pine	California
Stage	1973, 1979	Ponderosa pine, Douglas-fir, lodgepole pine, mixed western species	Northern Rocky Mountains, Pacific Northwest
USDA Forest Service	1979	Lake States species	Lake States
<u>Individual-tree distance-dependent models</u>			
Arney	1974	Douglas-fir	Pacific Northwest
Daniels and Burkhart	1975	Loblolly pine	Southeast
Daniels et al.	1979	Loblolly pine	South
Dress	1970	Even-aged pure species stands	Not geographically limited
Ek and Monserud	1974	Northern hardwoods	Lake States
Goldsmith	1976	Eastern white pine	Northeast
Hatch	1971	Red pine	Lake States
Hegyi	1974	Jack pine	Ontario
Lee	1967	Lodgepole pine	British Columbia, Alberta
Lin	1974	Douglas-fir, western hemlock	Pacific Northwest
Mitchell	1969	White spruce	New England
Mitchell	1975	Douglas-fir	Pacific Northwest
Newnham	1964	Douglas-fir	British Columbia
Newnham and Smith	1964	Douglas-fir, lodgepole pine	British Columbia

Appendix C.—Selected recent timber investment and cost studies by region of the United States and principal species

Author	Year	Principal species	Geographic area
<u>Timber investment studies</u>			
Adams and Ek	1974	Northern hardwoods	Lake States
Adams and Ek	1975	Northern hardwoods	Lake States
Amidon and Akin	1968	Loblolly pine	South
Anderson	1968	Southern pine	Georgia
Anderson and Guttenberg	1971	Oak-pine conversion to loblolly and slash pine	South
Beuter and Handy	1974	Douglas-fir	Western Oregon
Broderick et al.	1982	Loblolly pine	Virginia
Brodie et al.	1978	Douglas-fir	Pacific Northwest
Brodie and Kao	1979	Douglas-fir	Pacific Northwest
Callahan and Smith	1974	Black walnut	Midwest
Chappelle and Nelson	1964	Loblolly pine	South
Clawson and Hyde	1976	Douglas-fir	Coastal Pacific Northwest
Ek and Brodie	1975	Aspen	Lake States
Fight and Gedney	1973	Douglas-fir	Pacific Northwest
Flick et al.	1980	Loblolly pine	South (highlands)
Flora	1966	Ponderosa pine	Pacific Northwest
Forest Industries Council	1980	U.S. species	U.S.
Gansner and Herrick	1973	Upland oak	Ohio
Gedney et al.	1975	Pacific Northwest softwoods	Pacific Coast States
Hardie	1977	Loblolly pine	Mid-Atlantic
Herrick and Morse	1968	Appalachian forests	Virginia, W. Virginia
Hyde	1980	Douglas-fir	Pacific Northwest
Jackson and McQuillan	1979	Northern Rocky Mountain species	Montana
Knight and McClure	1974	Southern pine	Southeast
Koss and Scott	1978	Douglas-fir	Pacific Northwest
Leak	1980	Northern hardwoods	New England
Lewis and Chappelle	1964	Southern species	Virginia
Lundgren	1966	Red pine	Lake States
Manthy	1970	Softwoods/hardwoods	Pennsylvania
Marty	1973	Softwoods	U.S.
McCauley and Marquis	1972	Northern hardwoods	North
Mills	1976	U.S. species	U.S.

Appendix C.—Selected recent timber investment and cost studies by region
of the United States and principal species (continued)

Author	Year	Principal species	Geographic area
<u>Timber investment studies—continued</u>			
Randall	1977	Douglas-fir	Pacific Northwest
Row	1973	Southern pine	South
Row	1978	U.S. species	U.S.
Utz and Sims	1981	Upland oak	East
Vaux	1954	Sugar pine	California
Vaux	1973	California conifers	California
Webster	1960	White pine, Norway spruce	Pennsylvania
<u>Cost studies</u>			
Conkin	1971	Northern species	North
Cox	1980	U.S. species	U.S.
Hilliker et al.	1969	Lake States species	Lake States
Mills et al.	1982	U.S. species	U.S.
Moak and Kucera	1975	Southern species	South
Moak et al.	1977	Southern species	South
Moak et al.	1980	Southern species	South
Moak	1982	Southern species	South
Somberg et al.	1963	Southern species	South
Sunda and Lowry	1975	Loblolly pine	South
Weaver and Osterhaus	1976	Loblolly pine	South
Wikstrom and Alley	1967	Lodgepole pine	Montana, Idaho
Yoho	1961	Southern species	South
Yoho et al.	1969	Southern species	South

Appendix D.—Studies of retention and condition of timber investments
on private lands

Author	Year	Program	Geographic area	Practice type	Performance measure
Alig et al.	1980	Soil Bank	South	Pine plantations	Retention and condition
Kingsley and Mayer	1972	Mixture of cost share and private	North	Conifer plantations	Condition
Kurtz et al.	1980	Agricultural Conservation Program (ACP)	East	Conifer plantations	Retention and condition
Mills and Cain	1978	Forestry Incentives Program (FIP)	U.S.	Hardwood and conifer practices	Timber yield and financial return
Nodine and Marsinko	1979	Soil Bank	South Carolina	Pine plantations	Retention and condition
Risbrudt and Ellefson	1983	Forestry Incentives Program (FIP)	U.S.	Hardwood and conifer practices	Timber yield and financial return
Stone	1970	-----	Michigan	-----	-----
Tennessee Valley Authority (TVA)	1962	Soil Bank, ACP, CCC, private	Tennessee Valley	Pine and hardwood plantations	Retention and condition
Williston	1972	Yazoo-Little Tallahatchie Flood Prevention project	Northern Mississippi	Pine plantations	Retention and condition
Williston and Dell	1974	Civilian Conservation Corps (CCC)	Northern Mississippi	Pine plantations	Retention and condition

GLOSSARY

- DIAMETER CLASS:** A classification of trees based on tree diameter (including bark) measured at breast height (4-5 feet above the ground). D.b.h. is the common abbreviation for diameter at breast height, and 2-inch intervals or diameter classes are commonly used.
- DIRECT GROWTH AND YIELD MODEL:** Models in which the underlying sampling information is used directly as a basis for projecting forest development for a particular area or stand.
- EMPIRICAL YIELD TABLES:** Tabular presentation of the yield of stands or trees for average stand conditions under existing management practices.
- ENDOGENOUS VARIABLES:** Variables whose values are simultaneously determined by the model and which the model is designed to explain.
- ENGINEERING FUNCTION:** A function (or model) based on parameters estimated according to technical or engineering efficiency considerations.
- EXOGENOUS VARIABLES:** Variables originating from external causes, whose values are determined outside the model but influence the model.
- HARVEST FLOWS:** Annual or periodic estimates of timber that will be cut over time on a particular aggregate.
- HARVEST SCHEDULING:** A method for estimating a planned sequence of cutting and reforestation activities that are scheduled according to a prescribed norm, including the acres and volume harvested through each activity.
- INDIRECT GROWTH AND YIELD MODEL:** Models that are applied to subject stands or areas larger in nature than those from which the underlying sample growth and yield data was obtained, with two different sets of data used for model construction and application.
- NGROWTH:** Number of trees that grow into a particular timber-size class during a specified interval of time.
- NVENTORY:** Quantity of stumpage existing at a certain point in time for a specified geographical area (this term is also often used to refer to the activity of collecting data on the stock of timber).
- LONG RUN or LONG TERM:** A period of time in which all factors involved in the production process are considered variable.
- MARGINAL ANALYSIS:** Economic optimization principle that contribution to total revenue of an additional unit produced (i.e., marginal revenue) should equal the contribution to total cost of producing an additional unit (i.e., marginal cost).
- NORMAL YIELD TABLES:** Tabular presentation of the yield of "fully stocked," undisturbed natural stands by site-index and stand-age categories.
- NORMATIVE MODELING APPROACH:** Analytical framework designed to show what ought to be, given certain conditions and assumptions (i.e., prescriptive).
- POSITIVE MODELING APPROACH:** Analytical framework designed to describe things as they do exist or are likely to exist based on empirical or historical evidence (i.e., descriptive or predictive).
- PRECOMMERCIAL THINNING:** Removal of some unmerchantable trees from a forest stand to promote enhanced growth of the remaining trees.
- PRODUCTION FUNCTION:** Technical relationship between inputs and outputs in a production process; it is often expressed as an equation, as when the quantity of stumpage (output) is defined as a function of the relevant inputs (e.g., land).
- RESOURCES PLANNING ACT (RPA):** The Forest and Rangeland Resources Planning Act of 1974, which requires integrated planning between levels of state and federal agencies, including assessments at each level that culminate in a national assessment of the renewable resources.
- SAWTIMBER:** Live trees that are above a certain d.b.h. and contain merchantable lengths; for example, softwood sawtimber trees in the Pacific Northwest must be 11.0 inches in d.b.h. or larger and contain at least a 12-foot sawlog or two noncontiguous 8-foot sawlogs.
- SENSITIVITY ANALYSIS:** Procedure by which values for coefficients or variables are changed and the impact on a target value or solution observed. This technique is often used, for example, to see if an optimal solution is highly sensitive to the values used for variables that are not known with certainty.
- SHORT RUN:** Period of time in which one or more factors involved in the production process is considered fixed.
- STOCK:** Entire amount of standing timber existing at a particular point in time; it is also termed physical supply or inventory.
- STOCKING:** Degree of occupancy of land by trees, measured by basal area and/or number of trees by size or age and spacing, compared to a standard.
- TIMBER DEMAND:** Schedule of the quantities of stumpage that consumers are willing to purchase at different prices in a market specified as to time and place. Demand for stumpage is "derived" from the demand for other wood products such as lumber and plywood.
- TIMBER SUPPLY:** Schedule of the quantities of stumpage that producers are willing to offer for sale at different prices in a specific market area in a given time period.
- TIMBER SUPPLY ANALYSIS:** Examination and investigation of a timber supply complex, its elements, and their relations, in the context of a functional relationship between quantity of stumpage that would be supplied (or produced) and price.

Alig, Ralph J. 1984. Aggregate timber supply analysis. USDA Forest Service General Technical Report RM-106, 49 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Timber supply analysis techniques for broad geographical levels are summarized by land allocation, timber growth and yield, short-term harvest flows, and long-term timber investment modeling components. Representative techniques of these major analytical components are summarized in tabular form for supply regions. Aspects of uncertainty and aggregation in timber supply analyses are also discussed.

Keywords: Timber supply analyses, regional timber supply long-term timber supply projections

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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Flagstaff, Arizona
Fort Collins, Colorado*
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United States
Department of
Agriculture

Forest Service

Rocky Mountain
Forest and Range
Experiment Station

Fort Collins,
Colorado 80526

General Technical
Report RM-107



Empirical Estimates of Amenity Forest Values: A Comparative Review

Cindy F. Sorg and John B. Loomis



Empirical Estimates of Amenity Forest Values: A Comparative Review¹

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ABSTRACT

Comparisons of empirical estimates of the values of wildlife, wilderness, and general recreation require that the values are based on comparable methodologies and comparable units of measurements. Adjustments necessary to allow such comparisons are outlined and are applied to an extensive data base of valuation studies.

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¹Headquarters is in Fort Collins, in cooperation with Colorado State University.

Empirical Estimates of Amenity Forest Values: A Comparative Review

Cindy Sorg and John Loomis

INTRODUCTION

The focus of land management planning is changing, broadening from primarily a biological/ecological orientation to include economic efficiency considerations as an important component.

Recent emphasis at the federal level is to examine resource uses for economic utility. This report is designed to help land and natural resource management planners interpret wildlife, wilderness, and general recreation values derived using economic methodologies. After a brief discussion of methods used to derive these values, this report evaluates and summarizes the net values of wildlife, wilderness, and general recreation found in empirical studies since the mid-1960's, to allow comparison of values reported using different methodologies and different units of measurement. These values have been put on the same basis by adjusting for the effect of inflation on dollar values of earlier studies and by standardizing the methodology of all applications. The values also are now on an activity day basis, which is the amount of time in a day devoted to the primary activity. This standardization permits distinguishing differences in values resulting from resource quality-location from differences resulting from methodology.

METHODOLOGY

The data for this review came from published and unpublished information on recreation economics.

The studies relied on estimates of the net value (value in excess of actual expenditures) using primarily the Contingent Value Method (CVM) and Travel Cost Method (TCM). However, one study used the Household Production or "Hedonic Method" (Bell 1981), and one study used a "Hedonic-Travel Cost Method Synthesis" (Brown and Plummer 1979). Both of these approaches are new and promising valuation methodologies.

Because most of the empirical studies estimated the net value of a certain recreation activity at a specific site, given or adjusting for the availability of existing or substitute sites, the values reported represent marginal values for an additional recreation site, herd unit, stream, or wilderness area. The value represents net willingness to pay (i.e., average consumer surplus) for recreation. This is the appropriate value for efficiency analysis. The use of average consumer surplus is the appropriate measure when access to the site is not rationed by price but instead by user choice (Mumy and Hanke 1975, Loomis 1982a).

Advances in the theoretical foundation and empirical applications have provided the basis for a general non-market valuation framework within the context of microeconomic theory that provides "rules" for generating comparability between various applications of TCM and CVM (Bockstael and McConnell 1981, Brown et al. 1983).

Surveys of the literature are not substitutes for region-specific estimates of the value of recreation. These can be done using campground fee receipts, wilderness permits, and state game information as data sources for TCM. A few National Forests are already conducting TCM studies. A systematic effort to harness the existing data and skills within each Forest would provide more region-specific values for national forest plans.

In the preparation of this report, some empirical studies were rejected, because their results, in concept or in format were not relevant (e.g., dollar values on an annual basis). An initial set of adjustment criteria and size of each adjustment were formulated. Initial dollar values were calculated based on these adjustments. Then the adjustment criteria, size of adjustment, and values were submitted to a panel for review. The panel included William Brown, Oregon State University; David King, University of Arizona; Richard Walsh, Colorado State University; Elizabeth Wilman, Resources for the Future; and Dennis Schweitzer, Gary Elsner and Don Rosenthal, USDA Forest Service. Each member reviewed the adjustments and responded with comments. Considering their comments, the size of the adjustments were modified and the dollar values recalculated based on the new adjustment guidance. A discussion of the adjustment criteria and the size of the adjustment recommended by the panel follows.

Inappropriateness of Gross Expenditures

This method has been used extensively. The value of a recreation experience is alleged to equal the total amount of money spent by recreationists while participating in the activity. While insight into local income effects is provided, gross expenditures do not give an estimate of additional value created by an increase in recreation opportunities. Management decisions should be based on this net value in excess of the costs of taking advantage of the recreation opportunity, because this measures the real monetary value that would be lost if the opportunity were not available. What is needed is not a gross value but the net contribution to recrea-

tionists added by the recreation opportunity. Gross expenditures, while important locally, merely reflect transfers of expenditures from one area of the economy to another and are not net benefits. For example, in determining whether it is economically feasible to do some site improvement, such as planting trees in a picnic area, the management costs of planting must be compared to the benefits. Gross expenditures do not provide information on net benefits.

Travel Cost Method

This approach, first introduced by Hotelling (1949), was later used by Clawson (1959) to empirically estimate recreation benefits. The method is based on the premise that travel cost can be used as a proxy for price in derivation of a recreational site demand curve. The first step of a zonal TCM model involves dividing the area around the site into counties of origin. Using this origin data, a visitation rate (visits per capita) from each origin is calculated. Utilizing this visitation rate in conjunction with socioeconomic information for each origin, a first stage site demand curve can be estimated using regression analysis. Regression analysis involves relating visits per capita as a function of trip cost or distance, substitute sites, quality indexes, and various socioeconomic data. The second stage demand curve is derived by successively adding alternative hypothetical fees to each origin's travel cost, then estimating visits from each origin at each fee using the per capita demand curve. At a zero fee, net benefits is the total area under the demand curve (Johnson et al. 1981).

Contingent Valuation Method

This method is based on the notion of a bid curve (Bradford 1970). It involves directly asking individuals to give a measure of their consumer surplus by determining how much more a recreationist would be willing to pay for the recreation opportunity before going without the opportunity. Comprehensive reviews of this method are provided by Brookshire et al. (1980), and Schulze et al. (1981).

EVALUATION CRITERIA AND ADJUSTMENTS NECESSARY FOR COMPARABILITY OF VALUES

While nearly all of the studies reviewed are Travel Cost Method (TCM) or Contingent Value Method (CVM) studies (except as noted), some were performed before certain refinements in the methodology were developed, and others represented applications designed to highlight some aspect of resource valuation. Therefore, standardization of the resulting dollar values was necessary to allow the earlier, more developmental applications to be comparable to more recent applications. In addition, adjustment was necessary to bring 1965 or 1970 dollar values to 1982 dollar values.

The following types of adjustments are supported by the economic literature and were reviewed and approved by the panel.

1. For studies which did not report dollar values per day (e.g., per trip), put them on a per day basis.
2. Adjust dollar values to the January 1982 base year, using the GNP price deflator.
3. Adjust for omission of travel time in estimating TCM demand curve.
4. Adjust values derived by "individual observation" TCM for those activities where probability of participation is expected to vary significantly with travel cost.
5. Adjust values for restriction of TCM sample to in-state residents.
6. Adjust for omission of protest mechanism in CVM studies.
7. Report adjusted values by study location.

Most studies required only one or two types of adjustment.

Adjustment to Activity Day

Many studies reported values per "visitor day," "activity day," or "activity occasion." However, for the few studies that reported values per trip, conversion to an activity day was necessary. An activity day is that portion of the day devoted to the primary trip activity (i.e., picnicking activity day would possibly last four hours). If the studies reported a trip averaged 1.5 days, the value per trip was divided by 1.5. Because 1.5 days means that, on the average, 50% of the people spent 1 day, and 50% spent 2 days, this calculation produces a reasonable conversion from trips to days. Data on days per trip were derived from the studies themselves, by calling the study author(s), or by calling the appropriate State Fish and Game Department for an average length of hunting or fishing activities. Some studies reported recreation site value for the activity. This was divided by number of visitor days or trips to get value for the respective unit.

Updating Study Values to 1982

The nominal value of any consumer good or service, including recreation services provided by a Forest Service site, is expected to rise with the rise in the general price level. Therefore, to make the nominal values of studies performed at different dates useful for decision-making, all nominal values of recreation were adjusted to a common base year, January 1982, using the GNP implicit price deflator.

Adjustment for Travel Time

As early as 1965, researchers (Cesario and Knetsch 1970) became aware that omission of travel time from the travel cost model would lead to a substantial downward bias in the estimated benefits derived under the Travel Cost Method.

Time spent travelling can be viewed as the opportunity cost of not using the time in another activity. Consider a demand curve that reflects statistical estimation based on out-of-pocket travel costs only. If the cost to recreationists in County A was raised from \$5 to \$10 per trip, they would reduce visitations to the quantity taken by recreationists in County B. However, recreationists in County B incurred a price of \$10 Travel Cost and 1-hour travel time. Recreationists in County A, with the addition of \$5 to the original \$5, incur a travel cost of \$10, but still incur only their original travel time of 1/2 hour. Thus, the new price paid by recreationists in County A is still less than County B. Therefore, recreationists in County A would be expected to consume more visits at \$10 travel cost than recreationists in County B. This "time corrected" demand curve is outside the travel cost only demand curve. The value of recreation (measured as the area above the travel cost, but below the demand curve) is larger for the "time corrected" demand curve.

Because it is generally recognized that, for most recreation activities, the travel time price is just as important as the travel cost (Cesario and Knetsch 1970; Brown et al. 1973, Wilman 1980, McConnell and Strand 1981) much effort has gone into alternative ways of adjusting for travel time. The most direct method is to disaggregate the data into its original "individual observations" and then specify a separate independent variable. This was demonstrated by Brown et al. (1973) and has since been adopted by many other researchers (Martin et al. 1974, Ward 1982).

Another method has been to actually place a dollar value on time and add it to the travel costs (Cesario 1976). The value of travel time from commuting studies was estimated to be between one-fourth and one-half the wage rate (Cesario 1976). McConnell and Strand (1981), in a sport fishing application, found a value of 60% the wage rate. Bishop and Heberlein (1979) found that, when travel time was valued at one-half the hourly income rate, the TCM derived values began to come closer to the actual cash value of the goose hunting permit. Ward (1982) used a technique similar to that of McConnell and Strand (1981) to derive a value of travel time in southeastern New Mexico. He arrived at an average value of travel time of \$7.10 per hour.

Ward's work provides a starting point to begin actual adjustments for studies that omitted travel time. His work, along with that of Bishop and Heberlein (1979), showed that the magnitude of the benefit estimates vary with the change in value of travel time. Bishop and Heberlein (1979) found a 150% increase in the value of goose hunting when travel time went from a zero value (i.e., travel time omitted) to one-quarter of the hourly income rate. This is much higher than has been found in other studies. For example, Ward (1982) found that benefits increased by 60% when the value of travel time was increased from zero to 40% of his derived value of travel time.

While there near unanimity in the literature on the need to include travel time, the exact size of the correction of benefit estimates from studies which omitted travel time is not known with precision. For the purpose

of this report, a conservative 30% upward adjustment was used as an average for all activities.

Adjustment for Use of Individual Observation Travel Cost Method

Pioneered by Brown et al. (1973), the use of individual observations instead of zone aggregates as the dependent variables has gained widespread acceptability. The individual observation method uses trips or visits per year to site x by a given household or person as the dependent variable. Zonal TCM uses visits per capita from a county or zone of origin. As Brown et al. (1983) concluded, while the individual observation TCM is econometrically more efficient, it omits the effect of travel costs on the probability of participation. That is, as travel costs to a site increase, both the number of trips taken by participants and the number of participants per capita changes. This is consistent with the way Cicchetti (1973) dichotomized recreation use estimation processes. However, the individual observation method omits the effect of higher travel costs on lower probability of participation and leads to a more inelastic (steeper) demand curve (Brown et al. 1983). This more inelastic demand curve tends to result in overstating the recreation benefits, if the probability of participation decreases significantly at higher travel costs.

Because it is unlikely that probability of participation increases with higher travel costs, some downward adjustment in net value of recreation estimated by individual observation is necessary. The exact size of the downward adjustment depends on the degree to which probability of participation decreases with travel cost.

Since this change in probability of participation as a function of travel cost is likely to vary by activity, the 30% across the board downward adjustment that was suggested originally probably was, on average, too great. Instead, a range of downward adjustment between 0% and 30% was used. For activities in which individuals have acquired specialized equipment and skill, the probability of participation was less likely to be influenced by travel costs, therefore, no downward adjustment was made. However, for activities where specialized skill and equipment was not involved, a downward adjustment was made. To more accurately adjust individual observations, information is needed on how the probability of visiting a particular site varies with travel costs. Unfortunately, this information is not readily available.

Adjustment in TCM Studies for Restriction to In-state Users

One of the assumptions of the Travel Cost Method (TCM) is that, at each travel cost, any user who wishes to visit the site is not excluded. If out-of-state users are excluded from the survey, the visitation rate is not correct. Omission of out-of-state users tend to result in an underestimation of visits at relatively high travel costs. The effect on the demand curve and benefit estimates is

similar to that of omission of travel time. That is, benefits will tend to be underestimated to the degree that out-of-state users travel further distances than in-state users. This underestimate is further aggravated when the highest observed travel cost is used as the upper limit in deriving the second stage demand curve. If out-of-state users travel further than resident users, this omission in the sample TCM will further reduce benefits estimates. The above discussion applies to single site and single purpose out-of-state users.

Omission of out-of-state users was believed to be likely to produce the most serious underestimate of benefits for activities such as big game hunting, waterfowl hunting, cold water fishing, anadromous fishing, and boating. Therefore, values for these activities which omitted out-of-state users were adjusted by 15%.

Omission of Protest Mechanism in Contingent Valuation Method Studies

The Contingent Value Method is also known as the "bidding game" or direct survey method. CVM solicits a marginal value for recreating at a specific site, given the availability of alternative sites and activities. While the method has been criticized by some, Schulze et al. (1981), and Brookshire et al. (1982) provided substantial empirical evidence that CVM provides values consistent with economic theory and other methods of nonmarket valuation.

In recent CVM applications, it has been customary to include what is known as a "protest mechanism" to check to see if some proportion of the zero bids are rejection of the bidding game method itself or in fact zero value beyond current expenditures for the good under study. For example, use of taxes, utility bills, or license fees may be viewed as an inequitable way of paying for the good, because nonresidents or nonhunters/fishermen would benefit from provision without paying any costs. With these types of payment devices in particular, some zero "bids" may reflect a protest against this payment mechanism. If no cross check is done to investigate why persons bid zero, all zero bids are attributed to the resource value. The U.S. Water Resources Council (1979) indicated that the protest zero bids should not be included in value estimates, because they do not reflect benefits.

Because acceptable CVM applications are supposed to have no more than 15% of such protest bids (U.S. Water Resources Council 1979), an upward adjustment of up to 15% for omission of a protest mechanism was used for sensitive payment devices. Such payment devices include utility bills, taxes, and license fees.

ANADROMOUS FISHING

Literature Reviewed

Several studies have estimated net economic values for salmon and steelhead sport fishing in Oregon and salmon sport fishing in Washington (table 1). Brown et

Table 1.—Anadromous fishing methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Gordon (1970) Idaho 1968	17.00	41.70	54.21			54.21
Brown et al. (1980) Washington 1977	20.92	30.12			34.64	34.64
Brown et al. (1976) Oregon 1974	21.77	33.62			38.66	38.66
Brown et al. (1980) Oregon 1977	17.36	25.00			28.75	28.75
Matthews and Brown (1970) Washington 1967	38.75	99.02				99.02
Crutchfield and Schelle (1979) Washington 1978	18.00	25.92				25.92

al. (1976) reestimated data from an earlier study (Brown et al. 1964) of the zonal Travel Cost Method, using an adjustment for travel time. This also updated the base data from 1962 to 1974 dollars. Their estimate of \$21.77 per day was an average for Oregon salmon-steelhead fishing.

Matthews and Brown (1970) used the Contingent Value Method to estimate the value of salmon sport-fishing in Washington. They expressly addressed availability of substitutes when asking their value questions. They found an average value of \$38.75 in Washington.

A more recent zonal TCM application by Brown et al. (1980), yielded estimated values of \$17.36 per 3.3-hour day for an average in Oregon. The state average for Washington was \$20.92 per day, estimated using the zonal TCM. Both of these were based on a large mail survey of residents. The equations for Oregon considered the effect of travel time; but in Washington, only one of the three equations considered travel time.

A more recent CVM survey by Crutchfield and Schelle (1979) yielded a willingness to pay value of \$18.00 per day for ocean sport fishing in Washington.

A state average value of sport salmon fishing in Idaho, estimated using the zonal TCM, was \$17.00 a day (Gordon 1970). However, no adjustment was made for travel time.

Methodological Adjustments

Conversion of Values to 1982 Base Year

The updated Brown et al. (1976) values go from \$21.77 to \$33.62 (table 1). The updated Matthews and Brown (1970) value is \$99.02 per day. The Brown et al. (1980) value for Oregon is updated to \$25.00 and to \$30.12 for Washington per day. The Crutchfield and Schelle (1979) updated value is \$25.92 per day. Updating Gordons (1970) study using 1968 data to 1981, yielded a value of \$41.70 per day.

Adjustment for Omission of Travel Time

Two of the three Brown et al. (1980) TCM equations for Washington did not adjust for travel time. Because these were developed for less important salmon areas, no adjustment was made to the values contributed by these two equations.

Gordon's (1970) study in Idaho did not consider travel time. The updated value must be adjusted upward by 30% to \$54.21 per day (table 1).

Adjustment for Individual Observation TCM

Only the Brown et al. (1976) study utilized individual observation TCM. However, because the probability of participation in anadromous fishing probably did not have a strong inverse relationship to travel costs, no adjustment was made for this activity.

Adjustment for In-state Sample

For relatively unique activities, such as salmon fishing, the omission of out-of-state users was of particular concern. Thus, the values for Oregon and Washington need to be adjusted upward by 15%. Making this adjustment results in values of \$28.75 and \$34.64 for Oregon and Washington, respectively, for the Brown et al. (1980) values, and \$38.66 for Brown et al. (1976) value (table 1).

BIG GAME HUNTING

Literature Reviewed

Miller (1980) derived values for deer hunting in Colorado using both individual observation TCM and noniterative, open-ended CVM. The study derived separate values for resident and nonresident rifle hunting, resident sportsman hunting, muzzle-loading rifle hunting, and archery hunting. The TCM and CVM values reported here are for resident rifle hunting. The sportsman license no longer exists. Muzzle-loading and archery licenses represent a very small portion of total hunting. No TCM values were derived for nonresidents, but resident rifle hunting values were reported. A mail questionnaire was sent in 1974 to a random sample of license holders. The TCM values were adjusted for travel time but not substitutes. The CVM values represent willingness to pay additional costs to get to the hunt area but not additional costs at the hunt site. Values derived are \$9.11 and \$65.23 for CVM and TCM, respectively.

The individual observation TCM was used by Martin et al. (1974) to derive hunting values in Arizona. They reported a value for deer hunting and a value for all other big game hunting. The study adjusted for travel time and substitute sites. Data were collected in 1970 for in-state users only. A deer hunting value of \$52.85 was reported for a household trip. The average number of days per household trip was 1.9, resulting in a value of \$27.82 per household. The average number of people hunting in a household was 1.5, resulting in a value of \$18.54 per visitor day.

A value for all other big game hunting was reported as \$57.43. The average number of days per household trip was 1.9, resulting in a value of \$30.27 per household. The average number of people hunting in a household was 1.5, resulting in a value of \$20.15 per visitor days.

Loomis (1982a) used zonal TCM to derive the value of antelope hunting in Utah. Data were collected in 1979, but only in-state users were sampled. The study adjusted for travel time but not for substitute sites. A value of \$20.77 per trip was reported. Average trip length was 1.5 days, resulting in a value of \$13.80 per visitor day. Loomis (1982a) suggested that this value may be an underestimate of the true value because a linear functional form was used.

Hansen (1977) utilized CVM to derive values for deer, antelope, and elk hunting in the Intermountain Region.

Data were taken from the 1975 U.S. Fish and Wildlife Service Hunting and Fishing Survey. The mail survey format was noniterative, open-ended. Respondents were asked how much more they would be willing to spend before not engaging in the particular hunting activity in question. The following user day values were derived. Deer hunting was valued at \$20.55, antelope hunting at \$11.70, and elk hunting at \$22.63 per visitor day.

Deer hunting in Utah was valued by Wennergren et al. (1973) using zonal TCM. Data were collected in 1970 from an in-state sample. The study did not adjust for travel time or substitutes. The study reported a value of \$18.67 per trip. Average trip length was 2 days, resulting in a value of \$9.34 per visitor day.

Big game hunting in Idaho was valued by Brown and Plummer (1979) using a combination Hedonic-TCM. Data were collected in 1976. The study did not adjust for travel time or substitutes. An average state value of \$32.73 per activity day was reported.

Brown et al. (1973) measured the value of big game (deer and elk) hunting in Oregon. The study utilized individual observation TCM in a study which adjusted for travel time but not substitute sites. Instate mail sampling was done in 1968 from a list of hunters supplied by the Oregon State Game Commission. A value of \$9.20 per visitor day was reported.

The value of big game hunting in western Oregon was measured by Brown and Plummer (1979) by using the Hedonic-TCM. The study did not adjust for travel time or substitute sites. Based on data collected in 1976, a value of \$38.14 per activity day was reported.

Bell (1981) used the Hedonic method to value big game hunting in south-central Louisiana along the Atchafalaya River Basin. Data were taken from the 1975 U.S. Fish and Wildlife Service Hunting and Fishing Survey and the Atchafalaya Basin users survey. Bell's study did not adjust for travel time or substitute sites. A value of \$14.60 per visitor day is reported.

Utilizing individual observation TCM, Fisher (1982) measured the value of deer hunting in Pennsylvania. Data were collected in 1975. Fisher's study adjusted for travel time but not substitute sites. A value of \$80.00 per visitor day was reported. At first glance this value seems extremely high, but for what it measures and where it measures it, the value is reasonable. At the time of the study, Pennsylvania had a higher annual harvest of deer than any other state.

A national average value for deer hunting was derived using CVM, based on data collected in the 1980 U.S. Fish and Wildlife Service Hunting and Fishing Survey. The iterative personal interview questionnaire asked respondents how much more they would be willing to pay via change in trip costs for the 1980 hunting season. A value of \$24.00 per activity day was reported.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

The values for all big game hunting studies were converted to 1982 values, and are shown in table 2.

Adjustment for Omission of Travel Time

The studies by Wennergren et al. (1973), Brown and Plummer (1979), and Bell (1981), all omitted travel time in calculating values. Therefore, the values reported in these studies were increased by 30% (table 2).

Adjustment for Individual Observation

No downward adjustments for individual observation TCM were made for big game, because the probability of participation in big game hunting probably does not have a strong inverse relationship to travel costs.

Adjustment for In-state Sample

Because big game hunting in a given state often draws hunters from neighboring states, a 15% upward adjustment was made for studies which were limited to an in-state sample.

The studies by Miller (1980), Martin et al. (1974), Loomis (1982a), Wennergren et al. (1973), and Brown et al. (1973) all were based on in-state samples only. Therefore, all values reported by these studies were adjusted upward by 15% (table 2).

CAMPING

Literature Reviewed

Walsh et al. (1980a) found a value of \$13.72 for camping in underdeveloped sites near or adjacent to high mountain reservoirs in Colorado. They found an average value of \$10.90 per day for camping at developed sites near or adjacent to high mountain reservoirs. Both of these studies used a noniterative, open-ended Contingent Value Method approach during on-site interviews. In a second Colorado study, Walsh and Olienyk (1981), using an on-site survey and an iterative Contingent Value Method, found the value per day of developed camping to be \$5.59, and for semi-developed camping to be \$7.99 per day.

Martin et al. (1974) estimated the value of general outdoor recreation in Arizona. In this category, the average stay for camping was 1.4 days. Using an individual observation Travel Cost Method, they found a value of \$66.54 per household trip. Dividing by 1.4 days and 3.4 persons per household trip, the value per person per activity day was \$14.00. Their study adjusted for travel time.

Ward's (1982) study on recreation in southeastern New Mexico included sites in which there is developed camping. Using the individual observation TCM, Ward found an average value of \$11.39 per visitor day. His study also adjusted for the value of time.

Michaleson (1977) estimated the value of camping associated with river recreation in Idaho, using the individual observation TCM. He found an average value of \$9.00 per day. In another study using an individual

Table 2.—Big game hunting methodological adjustments

Author Study location Date of data species	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Miller (1980) Colorado 1974 deer (TCM)	65.23	114.61			131.80	131.80
Miller (1980) Colorado 1974 deer (CVM)	9.11	16.00			18.40	18.40
Martin et al. (1974) Arizona 1970 deer	18.54	40.91			47.05	47.05
Martin et al. (1974) Arizona 1970 other	20.15	44.46			51.13	51.13
Loomis (1982a) Utah 1979 antelope	13.80	17.11			19.68	19.68
Hansen (1977) Intermountain 1975 deer	20.55	33.03				33.03
Hansen (1977) Intermountain 1975 antelope	11.70	18.81				18.81
Hansen (1977) Intermountain 1975 elk	22.63	36.37				36.37
Wennergren et al. (1973) Utah 1970 deer	9.34	20.61	26.79		30.81	30.81
Brown & Plummer (1979) Idaho 1976 all	32.73	50.02	65.00			65.00
Brown et al. (1973) Oregon 1968 all	9.20	22.49			25.86	25.86
Brown and Plummer (1979) Oregon 1976 all	38.14	58.29	75.78			75.78
Bell (1981) Louisiana 1975 all	14.60	23.47	30.51			30.51
Fisher (1982) Pennsylvania 1975 deer	80.00	128.59				128.59
USFWS (1980) U.S. 1980 deer	24.00	27.32				27.32

observation Travel Cost Method, Michaleson and Gilmour (1978) found a value of \$3.73 per visitor day for outdoor recreation. Camping was the predominant activity (77% of respondents). They also adjusted for travel time. The data were collected in 1971 from on-site interviews.

Sutherland (1980) found an average value of \$4.23 per visitor day for camping in Oregon and Washington. This was estimated using a zonal TCM. He did not adjust for travel time, however, the study adjusted for substitutes. Brown and Plummer (1979) estimated the value of camping in western Washington at \$5.83 per day using a Hedonic TCM. They did not adjust for travel time. The data reflect on-site registration.

Gibbs (1974) used an unusual variant of the individual observation TCM to estimate the value of camping associated with river and lake recreation in Florida. his approach was to look at variations in on-site time as a function of cost per day. His value per trip was \$21.62.

The average length of trip was about 2 days. Thus, an average value was \$10.81 per visitor day. The study did not adjust for travel time.

Kalter and Gosse (1969) estimated the value of camping in New York using a zonal TCM. The estimated value of \$6.50 is a statewide average. Their study did not adjust for travel time, however.

Methodological Adjustments

Conversion of Values to 1982 Base Year

The values reported for all camping studies were converted to 1982 values, and are shown in table 3.

Adjustment for Omission of Travel Time

The TCM by Sutherland (1980), Brown and Plummer (1979), Gibbs (1974), and Kalter and Gosse (1969) all

Table 3.—Camping methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Walsh & Olienyk (1981) Colorado 1980	5.59-7.99	5.80-8.30				5.80-8.30
Walsh et al. (1980a) Colorado 1980	10.90-13.72	12.41-15.64				12.41-15.64
Martin et al. (1974) Arizona 1970	14.00	30.80		26.18		26.18
Ward (1982) New Mexico 1978	11.39	15.32		13.00	15.00	15.00
Michaleson (1977) Idaho 1971	9.00	18.93		16.00		16.00
Michaleson & Gilmour (1978) Idaho 1971	3.73	7.91		6.70		6.70
Sutherland (1980) Washington & Oregon 1980	4.23	4.81	6.25			6.25
Brown & Plummer (1979) Washington 1976	5.83	8.75	11.40			11.40
Gibbs (1974) Florida 1970	10.81	23.78	31.00	26.35		26.35
Kalter & Gosse (1969) New York 1965	6.50	14.30	18.60			18.60

omitted travel time. Therefore, the values reported for each of these studies were increased by 30% (table 3).

Adjustment for Individual Observation TCM

As discussed previously, values derived from individual observation TCM were adjusted downward slightly to make them consistent with values derived from zonal TCM (table 3).

Adjustment for In-state Sample

The value in Martin et al. (1974) was derived from a sample restricted to in-state users. Although this tends to understate the value somewhat, because camping is a regionalized activity, to be conservative, their value was not adjusted upward. However, in Ward's (1982) study, the survey was restricted to New Mexico counties near or adjacent to the sites under study. Because this is a much more drastic sample restriction, a 15% upward adjustment was made.

DOWNHILL SKIING

Literature Reviewed

Only one study dealt with the value of downhill skiing. Walsh² (1982) utilized the Contingent Valuation Method to derive a value estimation for downhill skiing at the Colorado areas of Vail, Copper Mountain, and Loveland Basin. Willingness to pay additional money in excess of current trip costs was the payment vehicle used. Data were collected in 1980 utilizing an iterative, in-person survey. A value of \$24.30 was reported. The study also reported that an average day of skiing at these areas was 5 hours.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

Walsh's (1982) value of \$24.30 converts to a 1982 value of \$30.13. No other adjustments were necessary for downhill skiing.

COLD WATER FISHING

Literature Reviewed

Three separate studies in Colorado utilized the Contingent Value Method to measure the value of cold water fishing. Walsh, et al. (1980a) utilized an in-person, noniterative, open-ended questionnaire which asked willingness to pay additional trip costs. Data for this study were collected in 1980. The study reports a value of \$10.90 per activity day.

²Letter to the White River National Forest.

In a second Colorado CVM study, by Walsh et al. (1980b), the questionnaire format was an in-person, noniterative, open-ended willingness to pay additional trip costs survey. Data were collected in 1980. A value of \$10.53 per activity day was reported.

The Walsh and Olienyk (1981) study differs from the others in that the in-person survey was used in an iterative format. As with the others, the payment vehicle was willingness to pay additional trip costs. Data were collected in 1980. A value of \$8.94 was reported for a 4.6-hour day.

King and Walka (1980) used an individual observation TCM in 1980, on the Fort Apache Indian Reservation, Arizona. The study did not adjust for substitutes or travel time. Updated values³ are \$221 per party trip. There were an average of 4.17 anglers per party, resulting in a value of \$53 per angler trip. A trip lasts an average of 5.8 days, resulting in a value of \$9.30 per angler day.

Individual observation TCM was also used by Martin et al. (1974) to derive a value for cold water fishing in Arizona. Data were collected in 1970. The study adjusted for substitutes and travel time. A value of \$50.13 per household trip was reported. The average length per household trip was 1.9 days, resulting in a value of \$26.38 per household per day. Average number of people per household trip was 2.6, resulting in a value of \$10.15 per activity day.

An Intermountain Region (Utah, Idaho, Western Wyoming, and Nevada) value was derived by Hansen (1977) utilizing CVM. Data were obtained from the 1975 U.S. Fish and Wildlife Service Hunting and Fishing Survey. This mail survey utilized the noniterative, open-ended format. Respondents were asked how much they were willing to spend before they would not engage in cold water fishing. The study reported a value of \$9.76 per activity day.

Gordon (1970) estimated the value of Idaho cold water fishing using the zonal TCM. Data were collected in 1968. The study did not adjust for substitutes or travel time. Gordon reported a value of \$3.65 per visitor day for cold water fishing on Idaho's high country lakes.

The U.S. Fish and Wildlife (1980) Hunting and Fishing Survey derived a value for trout fishing in Idaho. This personal interview utilized an iterative CVM format. Respondents were asked willingness to pay additional trip costs during the 1980 hunting and fishing season. A value of \$12.93 was derived for Idaho trout fishing.

Brown and Plummer (1979) used Hedonic-TCM to derive a value for cold water fishing in Washington and Oregon. Data were collected in 1976. The study did not adjust for substitutes or travel time. Values of \$19.00 and \$34.00 per visitor day were reported for Western Washington and Oregon, respectively.

A value for cold water fishing in Kentucky was derived by Bianchi (1969) using the zonal TCM. Fishermen were approached during the 1969 fishing season while they were engaged in fishing and given a survey to complete and return by mail. The study adjusted for travel time and substitutes within the state. A 150-mile zonal cut-off was used when deriving the demand curve. The study reported a value of \$3.51 per activity day.

³Personal Communication.

Weithman and Haas (1982) derived a value for cold water fishing in Lake Taneycomo, Missouri, utilizing the zonal TCM. The data were collected in 1979. The study adjusted for travel time but not substitute sites. A value of \$15.67 per visitor day was reported.

Kalter and Gosse (1969) derived a value of \$9.19 per visitor day for cold water fishing in New York. Data were collected in 1965. The study did not adjust for travel time or substitute sites.

Vaughan and Russell (1982) used the zonal TCM to derive a national value for trout fishing. Data were collected in 1979 using private fee fishing sites. The study adjusted for travel time and substitutes. When deriving the demand curve a 200-mile radius was used as the cutoff. A value of \$19.49 per activity day was reported.

The U.S. Fish and Wildlife (1980) Hunting and Fishing Survey derived a national average value for trout fishing. This personal interview utilized an iterative CVM format. Respondents were asked willingness to pay additional trip costs during the 1980 hunting and fishing season. A national average value of \$14.50 was reported.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

The values reported for all cold water fishing studies were converted to 1982 values, and are shown in table 4.

Adjustment for Omission of Travel Time

The cold water fishing studies by Gordon (1970), Brown and Plummer (1979), King and Walka (1980), and Kalter and Gosse (1969) did not include travel time in the values reported. Therefore, these values were increased by 30% (table 4).

Adjustment for Individual Observation TCM

No adjustment was made for individual observation TCM, because the probability of participation in cold water fishing does not exhibit a strong inverse relationship to travel costs.

Adjustment for In-state Sample

Cold water fishing is considered to be a regional or multi-state activity in some areas of the U.S.; therefore, an upward adjustment of 15% was made for studies which did not sample nonresidents (table 4).

WARM WATER (FRESH) FISHING

Literature Reviewed

Martin et al. (1974) utilized the individual observation Travel Cost Method to derive the recreational value of

warm water fishing in Arizona. Sampling in 1970 was restricted to in-state users only. Adjustments were made for travel time and substitutes. The study derived an average Arizona value of \$45.92 per household trip. The average number of days per household trip was 1.6, resulting in a value of \$28.70. The average number of people per household trip was 2.3, resulting in a visitor day value of \$12.48.

The individual observation TCM was used by Ziemer et al. (1980) for valuation of Georgia warm water fishing. The 1972 data were restricted to in-state sampling. The study adjusted for travel time but not substitute sites. A value of \$26.46 per trip was reported. Average trip length was 2 days, resulting in a value of \$13.23 per visitor day.

A study by Gibbs (1974) in Florida, used a variation of individual observation TCM. It was unusual because it used cost per day on site as the price variable. Data were collected in 1970. The study did not adjust for travel time or substitutes. Warm water fishing was valued at \$21.62 per trip. Average trip length was 2 days, indicating a value of \$10.81 per visitor day.

Warm water fishing was valued in south central Louisiana by Bell (1981) using the Hedonic Method. This study adjusted for travel time. Data were obtained in 1975 from the 1975 National Survey of Hunting and Fishing and The Atchafalaya Basin Users Survey. A value of \$15.98 per visitor day was reported.

Vaughan and Russell (1982) derived a national value for warm water fishing using the individual observation TCM. Data were collected in 1979. The study adjusted for both travel time and substitutes. A national value of \$14.09 was derived for warm water fishing.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

The values reported for all warm water fishing studies were converted to 1982 values, and are shown in table 5.

Adjustment for Omission of Travel Time

Gibb's (1974) Florida TCM study was the only study for which this adjustment is necessary. Adjusting the value of \$23.78 upward by 30% results in a value of \$31.00.

Adjustment for Individual Observation TCM

A slight downward adjustment of 15% was made for warm water fishing studies utilizing individual observation TCM, because this activity has a slight inverse relationship between the probability of participation and travel cost (table 5).

Adjustment for In-state Sample

Because warm water fishing is a localized activity, the Martin et al. (1974) study value, which is derived

Table 4.—Cold water fishing methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Walsh, et al. (1980a) Colorado 1980	10.90	12.41				12.41
Walsh, et al. (1980b) Colorado 1980	10.53	11.99				11.99
Walsh & Olienyk (1981) Colorado 1980	8.94	9.30				9.30
King & Walka (1980) Arizona 1980	9.30	10.59	13.75			13.75
Martin et al. (1974) Arizona 1970	10.15	22.39			25.75	25.75
Hansen (1977) Intermountain Region 1975	9.76	15.69				15.69
Gordon (1970) Idaho 1968	3.65	8.14	11.57			11.57
USFWS (1980) Idaho 1980	12.93	14.72				14.72
Brown & Plummer (1979) Washington 1976	19.00	29.04	37.75			37.75
Brown & Plummer (1979) Oregon 1976	34.00	51.96	67.55			67.55
Bianchi (1969) Kentucky 1969	3.51	8.58				8.58
Weithman & Haas (1982) Missouri 1979	15.67	19.43				19.43
Kalter & Gosse (1969) New York 1965	9.19	24.94	34.42		37.28	37.28
Vaughan & Russell (1982) US 1979	19.49	24.17				24.17
USFWS (1980) US 1980	14.50	16.50				16.50

Table 5.—Warm water (fresh) fishing methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Martin et al. (1974) Arizona 1970	12.48	27.54		23.41		23.41
Bell (1981) Louisiana 1975	15.98	25.69				25.69
Ziemer et al. (1980) Georgia 1972	13.23	26.71		22.70		22.70
Gibbs (1974) Florida 1970	10.81	23.78	31.00	26.35		26.35
Vaughan & Russell (1982) U.S. 1979	14.09	17.47		14.85		14.85

from in-state samples, does not need to be adjusted upward by 15%.

SALT WATER FISHING

Literature Reviewed

The only salt water fishing study found was for flounder fishing in Rhode Island. McConnell (1979) measured recreational salt water fishing values using both the Household Production (Hedonic Method) and the individual observation Travel Cost Method. Data were collected in 1978. The study adjusted for travel time but not substitutes. A value of \$30.34 and \$67.06 per visitor day was found using TCM and HM, respectively. McConnell identified a reason for the higher value associated with the Household Production. The quality variable is complementary to trips; thus, leaving out either of these variables results in a strong downward bias in the results. The Travel Cost Model does not contain a quality variable; as a result, this measure is an underestimate.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

The values for salt water fishing in Rhode Island convert to 1982 values of \$40.81 and \$90.19 for TCM and HM, respectively.

Adjustment for Individual Observation TCM

Because in the case of salt water fishing, the probability of participation does not have a strong inverse related to travel cost, no adjustment is necessary.

HIKING

Literature Reviewed

Walsh et al. (1980a) found hiking-backpacking values associated with remote undeveloped high mountain reservoirs in Colorado. Using on-site interviews and a noniterative open-ended Contingent Value Method, they found the value as \$13.72 per activity day. Walsh and Olienyk (1981) used an on-site iterative Contingent Value Method to estimate the value of hiking and backpacking along the Front Range of Colorado. They found a value of \$9.51 for a 4-hour hiking day and \$9.36 for a 5.6-hour backpacking day. Rosenthal⁴ (1982) using on-site iterative Contingent Value Method, found an average value of \$7.55 per RVD.

Martin et al. (1974) estimated the value of general rural outdoor recreation in Arizona. Hiking was listed as the second most frequent activity. Martin et al. (1974) used the individual observation Travel Cost Method. The data came from a household survey of Arizona residents. They adjusted for travel time. The value reported was \$66.54 per household trip. There were 3.4 persons per household trip, and each trip lasted an average of 1.4 days. The value per activity day was \$13.97.

Brown and Plummer (1979) estimated the value of hiking and backpacking in western Washington. They used a hedonic-TCM, but did not adjust for travel time. The value per recreation day is \$9.40. Their data were based on on-site visitor registration.

Kalter and Gosse (1969) estimated an average value of hiking in New York using the zonal TCM. They did not adjust for travel time. Their data were from Bureau of Outdoor Recreation household survey. Their value was \$16.00 per day.

⁴Letter to Dr. Andrew Farkas, U.S. Department of Agriculture, Forest Service, Washington, D.C.

Conversion of Values to a 1982 Base Year

The values reported for all hiking and backpacking studies were converted to 1982 values, and are shown in table 6.

Adjustment for Omission of Travel Time

Both the Brown and Plummer (1979) study and Kalter and Gosse (1969) study omitted travel time. As discussed in the introduction, the values reported were increased 30% to correct for this omission (table 6).

Adjustment for Individual Observation TCM

The values in Martin et al. (1974) were adjusted downward slightly to make it consistent with zonal TCM derived values (table 6).

Adjustment for In-state Sample

While the Martin et al. (1974) survey was restricted to Arizona residents, for national forest hiking, this may not result in a substantial underestimation of dollar values. This is because hiking is a more regionalized activity, at least given the national forest resource attractiveness in Arizona. Therefore, to be conservative, this value was not adjusted upward.

Literature Reviewed

Ward (1982) estimated an average value of \$11.39 per day for motorized boating at reservoirs in southeastern New Mexico using an individual observation Travel Cost Method. He adjusted for substitutes and travel time. The household survey was restricted to only neighboring counties.

Sutherland (1980) estimated the average value of motorized boating in Oregon and Washington using a zonal TCM. He did not adjust for travel time, however. His average value was \$4.24 per day.

Kalter and Gosse (1969) used a zonal TCM to estimate the average value of motorized boating in the State of New York. Their study did not adjust for travel time. They found an average value of \$15.14.

Methodological Adjustments**Conversion of Values to a 1982 Base Year**

Updating the Ward (1982), Sutherland (1980), and Kalter and Gosse (1969) studies to 1982 yields value of \$15.32, \$4.83, and \$33.40 per activity day, respectively.

Adjustment for Omission of Travel Time

The Sutherland (1980) study omitted travel time; therefore, making a 30% upward correction yields a

Table 6.—Hiking methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Walsh et al. (1980a) Colorado 1980	13.72	15.62				15.62
Walsh & Olienyk (1981) Colorado 1980	9.36-9.51	10.67-10.84				10.67-10.84
Rosenthal (1982) Colorado 1981	7.55	8.25				8.25
Martin et al. (1974) Arizona 1970	13.97	30.80		26.00		26.00
Brown & Plummer (1979) Washington 1976	9.40	14.00	18.20			18.20
Kalter & Gosse (1969) New York 1965	16.00	35.20	45.76			45.76

value of \$6.28. The Kalter and Gosse (1969) value also was increased 30% yielding a value of \$43.42 per activity day.

Adjustment for Individual Observation TCM

As discussed previously, a downward adjustment is necessary to make values derived from individual observation TCM consistent with zonal TCM. Because the probability of participation in motorized boating is likely to be equally affected by travel cost as by ownership of equipment, a slight downward adjustment is necessary. Therefore, Ward's (1982) value was adjusted to \$13.00 per activity day.

Adjustment for In-state Sample

Ward's (1982) sample was restricted to just counties adjacent to the reservoirs. More distant counties and acknowledged out-of-state residents (Texas) were omitted from sampling. While motorized boating at reservoirs is somewhat of a regional activity, these more distant observations are still important. Therefore, an adjustment to \$14.00 per activity day was made.

MOTORIZED TRAVEL

Literature Reviewed

The only study found for motorized recreation was an outdoor recreation vehicle study done on Forest Service land in Colorado. Walsh and Olienyk (1981) reported a value of \$6.45 for a visit lasting 4.2 hours. This study utilized the Contingent Value Method. It was an on-site interview using iterative bidding. The payment vehicle was change in trip costs.

Methodological Adjustments

Conversion of Value to 1982 Base Year

Conversion to 1982 base year increased the reported value to \$6.70. No other methodological adjustments are necessary.

NONMOTORIZED BOATING

Literature Reviewed

Walsh et al. (1980b) used a noniterative, open-ended Contingent Value Method to estimate the average value of rafting and kayaking on nine rivers in western Colorado. The value per day was \$12.65 for kayaking and \$10.94 for rafting. The 206 interviews took place on site.

Keith et al. (1982) found a value of \$23.79 per day using the individual observation Travel Cost Method for recrea-

tional floating in Arizona. The "put-in" point on this river is on Forest Service land. The data necessary to do the analysis were collected from on-site interviews.

Michaleson (1977) estimated the value of floating the Middle Fork of the Salmon River and several non-wild and scenic rivers in Idaho. The value per day for the Middle Fork of the Salmon River was \$76.85 per activity day. The average value for the other rivers was \$10.36. Michaleson used the individual observation TCM. His study adjusted for travel time.

Bowes and Loomis (1980) estimated the values of white water rafting, kayaking, and floatboating on the Westwater Canyon portion of the Colorado River in Utah. They used a zonal TCM, but did not adjust for travel time. Their value was \$19.00 per activity day. The data came from trip permits.

Sutherland (1980) estimated the value of boating in Oregon and Washington using the zonal TCM. He did not adjust for travel time, however. Sutherland found an average value of \$4.24 per day.

Methodological Adjustment

Conversion of Values to a 1982 Base Year

The values reported for all nonmotorized boating studies were converted to 1982 values, and are shown in table 7.

Adjustment for Omission of Travel Time

Because the Sutherland (1980) and Bowes and Loomis (1980) values did not adjust for travel time, they were increased 30% resulting in values of \$6.28 and \$33.22 per day, respectively.

Adjustment for Individual Observation TCM

The probability of participating in nonmotorized boating may be influenced as much by travel costs as by ownership of specialized equipment and possession of requisite boating skills. Therefore, a small downward adjustment of Michaleson's (1977) and Keith's (1982) individual observation TCM values is necessary to make them comparable to zonal TCM values (table 7).

PICNICKING

Literature Reviewed

The most explicit study of picnicking was done by Walsh and Olienyk (1981) using on-site iterative Contingent Value Method. They found a value of \$6.22 per 4.2 hour day. This study was done at several sites along the Front Range in Colorado.

Another Colorado study was of picnicking related recreational use of developed and semi-developed high

Table 7.—Nonmotorized boating methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Walsh et al. (1980b) Colorado 1980	10.94–12.65	14.65–16.95				14.65–16.95
Keith et al. (1982) Arizona 1981	23.79	24.79		21.00		
Michaleson (1977) Idaho 1969, 1971	76.85–10.36	176.00–21.85		150.00–18.50		150.00–18.50
Bowes & Loomis (1980) Utah 1978	19.00	25.55	33.22			33.22
Sutherland (1980) Washington-Oregon 1980	4.24	4.83	6.28			6.28

mountain reservoirs (Walsh, et al. 1980a). Using on-site, noniterative, open-ended CVM, they found an average value for these two types of reservoirs of \$10.90 per day.

Martin et al. (1974) estimated the value of general rural outdoor recreation in Arizona using the individual observation Travel Cost Method. One of the dominant activities was picnicking. This was a household survey limited to residents only. Martin et al. (1974) found a value of \$66.54 per household trip. There were 3.4 people per household trip, resulting in a value per person per trip of \$19.57. Since most trips taken primarily for picnicking are 1 day or less in duration, this becomes the value per day. Their study adjusted for travel time and tested for substitutes.

Ward (1982) estimated the value of recreation at several reservoirs in southeastern New Mexico. Because these reservoirs include state parks, some near population centers, picnicking may be one of the most frequent activities. Ward used an individual observation TCM to estimate a value of \$11.39 a day. While the sample was restricted only to counties adjacent to each reservoir under study, this limitation is not of too great a concern for a localized activity such as picnicking. This model adjusted for travel time and substitutes.

Knetsch et al. (1976) estimated the value of day trips to California reservoirs using a regional zonal Travel Cost Method. Their model reflected travel time and substitute sites. Again, picnicking reflected a large proportion of the use at these reservoirs. This study estimated an average of \$3.33 in 1969.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

The values reported for all picnicking studies were converted to 1982 values, and are shown in table 8.

Adjustment for Omission of Travel Time

None of the TCM studies omitted travel time.

Adjustment for Individual Observation TCM

As discussed previously, a downward adjustment is necessary for studies that used individual rather than zonal TCM when probability of participation is strongly related to travel costs. Picnicking is probably one of those activities. Thus, the Martin et al. (1974) and Ward (1982) values must be adjusted downward by 30% (table 8).

Adjustment for In-state Sample

While the Martin et al (1974) study was restricted to in-state samples, this is not a serious bias for a localized activity such as picnicking. The restriction of Ward's (1982) sample to counties adjacent to the reservoir is more of a concern, but to be conservative, no adjustment was made. However, this factor should be taken into consideration when reconciling the two different study values.

SMALL GAME HUNTING

Literature Reviewed

Martin et al. (1974) utilized the individual observation Travel Cost Method to derive the value of small game hunting in Arizona. Data were collected in 1970, and sampling was restricted to in-state users. Adjustment for substitutes and travel time were made in the study. The study reported a statewide average value of \$23.89 per household trip. The average days per household per trip was 1.1, resulting in a value of \$21.72 per house-

Table 8.—Picnicking methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Walsh & Olienyk (1981) Colorado 1980	6.22	6.53				6.53
Walsh et al. (1980a) Colorado 1980	10.90	12.41				12.41
Martin et al. (1974) Arizona 1970	19.57	42.61		28.54		28.54
Ward (1982) New Mexico 1978	11.39	15.32		10.26		10.26
Knetsch et al. (1976) California 1969	3.33	7.75				7.75

hold. The average number of persons per household trip was 1.5, resulting in a value of \$14.48 per visitor day.

Brown and Plummer (1979) utilized the zonal TCM, in combination with the Hedonic Method, to allow for better utilization of available data. Data was obtained from the 1976 Recreation Information Management System (RIM) and the 1976 RARE II analysis. This Idaho study did not adjust for travel time or substitutes. The study reported a value of \$21.43 per visitor day.

An Intermountain (Utah, Idaho, Western Wyoming, and Nevada) value was obtained by Hansen (1977) utilizing data from the 1975 U.S. Fish and Wildlife Service Hunting and Fishing Survey. The Hunting and Fishing Survey used a noniterative, open-ended contingent value mail questionnaire. The study reported a regional value of \$13.95 per visitor day.

Bell (1981) utilized the Hedonic Method to derive small game hunting values for the south-central portion of Louisiana. Data from the 1975 National Survey of Hunting and Fishing, along with the Atchafalaya Basin Users Survey were analyzed. The study adjusted for substitutes and travel time. A value of \$9.79 per visitor day was reported.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

The values reported for all small game hunting studies were converted to 1982 values, and are shown in table 9.

Adjustment for Omission of Travel Time

The Idaho study done by Brown and Plummer (1979) is the only TCM study which did not adjust for travel time. The value of \$32.75 was increased by 30% to \$42.58.

Adjustment for Individual Observation TCM

The Martin et al. (1974) study was the only study examined which utilized individual observation TCM. Because the probability of participation in small game hunting is inversely related to travel cost, the value was adjusted downward to \$23.93.

UPLAND GAME HUNTING

Literature Reviewed

Only one study dealt with valuation of upland game hunting. Hansen (1977) utilized data from the 1975 U.S. Fish and Wildlife Service Hunting and Fishing Survey to derive a region wide average value for all states in the Intermountain Region. The Hunting and Fishing Survey used a noniterative, open-ended, contingent value mail questionnaire. Other than a lower than desirable return rate (30%), the study is acceptable. Only the new willingness to pay values from Hansen's study are reported here. An average dollar value of \$23.06 per activity day was derived.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

Hansen's 1975 value of \$23.06 converts to a 1982 value of \$37.06. No other adjustments were necessary.

WATERFOWL HUNTING

Literature Reviewed

Brown and Hammack (1972) used the Contingent Valuation Method to derive a value for waterfowl hunting

Table 9.—Small game hunting methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Martin et al. (1974) Arizona 1970	14.48	31.95		23.93		23.93
Hansen (1977) Intermountain 1975	13.95	22.42				22.42
Brown & Plummer (1979) Idaho 1976	21.43	32.75	42.58			42.58
Bell (1981) Louisiana 1975	9.79	15.74				15.74

in the Pacific Flyway. Their CVM study was a mail, non-iterative open-ended questionnaire. Respondents were asked willingness to pay additional costs during the waterfowl season. Data were collected in 1968. A value of \$256.00 per hunter was reported. A hunter spent an average of 10.5 days in the field during the season, resulting in a value of \$25.00 per activity day.

Using individual observation Travel Cost Method, Martin et al. (1974) derived a value for waterfowl hunting in Arizona. Data were collected in 1970. Substitutes and travel time were adjusted for in the study. A value of \$9.87 per household trip was reported. The average days per household per trip was 1.1, resulting in a value of \$8.97 per household per day. The average number of people per household trip was 1.4, resulting in a value of \$6.41 per visitor day.

An Intermountain Region value was derived by Hansen (1977) using the CVM. Data were obtained from the 1975 U.S. Fish and Wildlife Service Hunting and Fishing Survey. The mail survey was noniterative, open-ended questionnaire. A value of \$20.12 per visitor day was reported.

Waterfowl hunting in a marsh area of south-central Louisiana was valued by Bell (1981), using the Hedonic Method. Data from the 1975 National Survey of Hunting and Fishing and the 1975 Atchafalaya Basin Users Survey were analyzed. The study adjusted for substitutes and travel time. A value of \$15.41 per visitor day was reported.

Bishop and Heberlein (1980) valued goose hunting in Wisconsin using several methodologies. Each method, however, derived a value for a goose hunting permit. A value of \$63.00 represents the average cash payment accepted to give up a goose hunting permit. The format involved checks from \$1 to \$200 sent to current holders of permits. They could either accept the check and give up the permit or vice versa. A second sample was asked their hypothetical willingness to pay additional money for a permit. The survey format was a closed-ended non-iterative mail questionnaire. This resulted in an average

net willingness to pay of \$21.00 per permit. A third sample was asked questions which allowed implementing the zonal TCM. The TCM results ranged from \$7.00 per permit, when no adjustment was made for travel time, to \$32.00 per permit when travel time was valued at ½ the wage rate. Data for each method were collected in 1978.

Methodological Adjustment

Conversion of Values to a 1982 Base Year

The values reported for all waterfowl hunting studies were converted to 1982 values, and are shown in table 10.

Adjustment for Individual Observation TCM

Because the probability of participation in waterfowl hunting is not inversely related to travel cost, no adjustment was made for studies which utilized individual observation TCM.

Adjustment for In-state Sample

Waterfowl hunting is considered to be a multi-state activity. As a result, values from studies which were limited to an in-state sample were adjusted upward by 15%. This adjustment is necessary only in the case of the Martin et al. (1974) study (table 10).

WATER SPORTS

Literature Reviewed

Ward (1982) used the individual observation Travel Cost Method to value lake and reservoir water-based

Table 10.—Waterfowl hunting methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Martin et al. (1974) Arizona 1970	6.41	14.14			16.26	16.26
Hansen (1977) Intermountain 1975	20.12	32.34				32.34
Brown & Hammack (1972) Pacific Flyway 1968	25.00	61.11				61.11
Bell (1981) Louisiana 1975	15.41	24.77				24.77
Bishop and Heberlein (1980) Wisconsin 1978 cash	63.00	84.73				84.73
Bishop and Heberlein (1980) Wisconsin 1978 CVM	21.00	28.24				28.24
Bishop and Heberlein (1980) Wisconsin 1978 TCM	32.00	41.66				41.66

recreation in southeastern New Mexico. Data were collected in 1978. Substitutes and travel time were adjusted for in the TCM application. An average dollar value of \$11.39 per activity day was derived.

Martin et al. (1974) studied general outdoor recreation, which included water sports. They derived a statewide average for Arizona using the individual observation TCM. Substitutes and travel time were adjusted for in the TCM application. A value of \$66.54 was found per household per trip. The average number of days per trip was 1.4, and number in household was 3.4 persons. The resulting value was \$13.98 per visitor day.

Grubb and Goodwin (1968) used the zonal TCM to derive water sport values in Texas. Data were collected in 1965. Adjustments were made in the study for substitutes; however, no adjustments were made for travel time. An average value of \$3.80 per visitor day was found.

In Florida, Gibbs (1974) ran a variant of the individual observation Travel Cost Method for lake and stream recreation. Data were collected in 1970. This TCM study was unusual, because it used cost per day on site as the price variable. The value derived was \$21.62 per 2-day trip, resulting in a value of \$10.31 per visitor day.

Kalter and Gosse (1969) valued swimming in New York using the zonal TCM. The study did not adjust for substitutes or travel time. An average value of \$9.47 per day was derived.

Methodological Adjustment

Conversion of Values to a 1982 Base Year

The values reported for all water sports studies were converted to 1982 values, and are shown in table 11.

Adjustment for Omission of Travel Time

The study values which omitted travel time were adjusted upward by 30% (table 11).

Adjustment for Individual Observation TCM

Water sport studies which derived values using individual observations were adjusted downward, because there is a strong inverse relation between probability of participation and travel cost (table 11).

WILDERNESS

Literature Reviewed

Perhaps the best empirical estimates for wilderness recreation has been done in Colorado. Walsh and

Table 11.—Water sports methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Martin et al. (1974) Arizona 1970	13.98	30.84		20.66		20.66
Ward (1982) New Mexico 1978	11.39	15.32		10.26		10.26
Grubb & Goodwin (1968) Texas 1965	3.80	10.31	13.40			13.40
Gibbs (1974) Florida 1970	10.31	23.78	31.00	20.65		20.65
Kalter & Gosse (1969) New York 1965	9.47	20.83	27.00			27.00

Gilliam (1982) applied the Contingent Value Method to estimate benefits of wilderness hiking and backpacking in Indian Peaks Wilderness Area in Colorado. This was an on-site personal interview that used the CVM with an iterative bidding format. They reported values associated with a wide range of different levels of congestion. They presented the mean congestion levels for hiking and backpacking, which were used to locate the appropriate dollar values. These values were \$10.31 for hiking per activity day and \$18.29 for backpacking per activity day.

Walsh et al. (1981) calculated a statewide average value for wilderness and roadless area recreation using the individual observation Travel Cost Method. This was based on a sample of more than 200 state residents. Travel time, substitutes, tastes-preferences, and income were all accounted for and included in the regression when statistically significant. The study found a value of \$14.00 per visitor day.

Loomis (1979, 1980) estimated the hiking and backpacking values associated with two administratively designated primitive areas in southern Utah. Using the zonal TCM, the values were \$8.00 per visitor day for Grand Gulch and \$15.00 per visitor day for Paria Canyon. An overall average of \$11.50. No adjustment was made for travel time, however. Because these were high desert, primitive areas, the justification for using these studies rests on the concept of Recreation Opportunity Spectrum (ROS) zones. That is recreation opportunities that share the same ROS classification provide a similar experience even if the ecosystem is different. Further research in this region is needed.

Smith and Kopp (1978), using 1972 data, estimated that the average recreation value per visit to the Ventana Wilderness in California was \$10.04, with in-

dividual estimates ranging between \$5.28 and \$14.80 depending on the assumptions made about the maximum distance for single purpose trips. However, these authors used only one way distance, and did not adjust for travel time. Because it is well established that round trip distance or travel cost is necessary (Dwyer et al. 1977, Walsh 1977), adjustment is necessary even before the omission of travel time can be corrected later. In a footnote to the longer version of this Smith and Kopp (1980) paper, they indicated that to recalculate their consumer surplus figures to adjust to round trip mileage, one can just double the benefit estimates. Doing this results in a value of \$20.08 per visit before adjusting for travel time. Putting this on a per visitor day basis, using data provided by the District Ranger, results in a value of \$8.03 per RVD in 1972.

Using a zonal TCM, Brown and Plummer (1979) estimated the wilderness recreation value for wilderness areas in Washington and Oregon. The values per day were \$40.00 for Glacier Peak, \$37.00 for Goat Rocks, \$44.00 for Diamond Peak, and \$54.00 for Eagle Cap. This results in an overall average of \$43.75. However, this study did not adjust for travel time. These values reflect an upper limit truncation made by Brown and Plummer (1979) to insure single purpose trips. The values without this upper limit truncation were \$100.00 per day. The data for the zonal TCM reflects both in-state and out-of-state residents.

Methodological Adjustments

Conversion of Values to a 1982 Base Year

The values reported for all wilderness studies were converted to 1982 values, and are shown in table 12.

Table 12.—Wilderness methodological adjustments

Author Study location Date of data	Reported value/ Activity day	Adjustment to 1982	Adjustment to include travel time	Adjustment for individual observation	Adjustment for in-state only	Adjusted values/ Activity day
Walsh & Gilliam (1982) Colorado 1979	10.31-18.29	12.78-22.68				12.78-22.68
Walsh et al. (1981) Colorado 1980	14.00	15.93		18.32		18.32
Loomis (1979-1980) Utah 1979	11.50	14.95	19.45			19.45
Smith and Kopp (1980) California 1972	8.03	15.79	20.50			20.50
Brown & Plummer (1979) Washington, Oregon 1976	43.75	56.87	73.93			73.93

Adjustment for Omission of Travel Time

The study values from Loomis (1979, 1980), Smith and Kopp (1980), and Brown and Plummer (1979) were adjusted to correct for omission of travel time (table 12).

Adjustment for In-state Sample

Only Walsh et al. (1981) limited the survey to an in-state sample. Because wilderness areas in Colorado draw from a multistate area, a 15% upward adjustment was made (table 12).

CONCLUSION

The recreation values estimated using different methods and in different locations are fairly consistent when the methodological assumptions and dates of studies are standardized. The differences in value that exist can be largely explained by differences in resource quality and relative location from user populations. For example, the \$20.50 for the Ventana Wilderness (Smith and Kopp 1980), represents a value for a non-alpine, relatively small wilderness area 135 miles from the San Francisco Bay area and more than 250 miles from the Los Angeles area. The Walsh and Gilliam (1982) \$12.78-\$22.68 value reflects a large alpine wilderness area within 65 miles of Denver, Colo. The \$15.93 represents a state average for wilderness and roadless areas in Colorado well within the Walsh and Gilliam (1982) range. There appears to be a reasonable degree of consistency across methods since the Walsh and Gilliam (1982) study of Colorado Wilderness used an iterative bidding game and Walsh et al. (1981) used a

Travel Cost Method. The values also seem to reflect site location and quality. Without the necessary methodological adjustments, such conclusions would be difficult to draw.

Cold water fishing represents another example of values, once methodologically adjusted, that are fairly similar for comparable quality and location (see table 4). The wilderness and cold water fishing examples show the importance of standardizing values across studies. Values which appeared inconsistent initially became more comparable once methodological, quality and location adjustments are made. To better allow for scientific comparisons between studies over time and to ease adoption of research results by federal and state resource agencies, greater consistency in reporting results is needed. At a minimum, researchers should explicitly define the unit of recreation output. What is meant by a trip or visit? Length of stay and the number in the party is crucial information if the information is to be utilized by federal agencies. Another issue is travel time. Was travel time valued and at what rate? What assumptions were made about spatial limits, either in sampling or in statistical estimation? By providing this type of information, recreation benefit estimates may become more useful.

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

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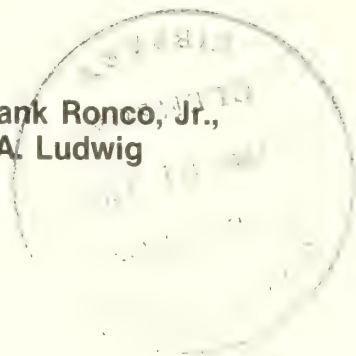
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General Technical
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Douglas-fir Habitat Types of Northern Arizona

Billy G. Alexander, Jr., Frank Ronco, Jr.,
Alan S. White, and John A. Ludwig



Abstract

Four Douglas-fir (*Pseudotsuga menziesii*) habitat types and two phases were identified from a reconnaissance survey of 46 Douglas-fir stands in northern Arizona. General descriptions of these habitat types are presented, and a key to their identification is provided.

Douglas-fir Habitat Types of Northern Arizona¹

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Contents

	Page
INTRODUCTION	1
STUDY AREA	1
METHODS	2
Field Sampling	2
Data Analysis	2
RESULTS AND DISCUSSION	2
<i>Pseudotsuga menziesii</i> /Muhlenbergia virescens habitat type	3
<i>Pseudotsuga menziesii</i> /Festuca arizonica habitat type	4
<i>Pseudotsuga menziesii</i> /Quercus gambelii habitat type	5
<i>Pseudotsuga menziesii</i> /Sparse undergrowth habitat type	6
CONCLUSIONS	8
LITERATURE CITED	8
APPENDICES	9
Appendix A. —Key to the series level and <i>Pseudotsuga menziesii</i> habitat types of northern Arizona	9
Appendix B. —Plant list from sampled <i>Pseudotsuga menziesii</i> stands in northern Arizona	10
Appendix C. —Table of average cover and constancy of major species in <i>Pseudotsuga menziesii</i> habitat types in northern Arizona ..	12

Douglas-fir Habitat Types of Northern Arizona

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INTRODUCTION

Habitat type classification, originally developed for northern Idaho and eastern Washington by Daubenmire (1952), has been extended to many areas of the West (Pfister 1977, Pfister 1981, Steele et al. 1981). Such a classification provides a natural means for dividing diverse forest conditions into an hierarchical system that establishes a basis for communication, especially regarding responses of the ecosystem to management activities. Habitat types describe areas of land that are capable of supporting the same plant associations. Although such associations represent the potential climax vegetation, existing vegetation within a habitat type may be quite variable, reflecting different stages of successional development (Arno and Pfister 1977).

Layser and Schubert (1979) described coniferous and woodland series, the hierarchical level classified by the potential climax overstory. Within these series, limited descriptions of habitat types have been published for the spruce-fir (*Picea-Abies*)² and mixed conifer types (Moir and Ludwig 1979) and ponderosa pine (*Pinus ponderosa*) types (Hanks et al. 1983). Other studies are being conducted to describe the habitat types within all coniferous forest series of selected geographic units. The objectives of the study reported here were to determine existing habitat types in the Douglas-fir (*Pseudotsuga menziesii*) series of northern Arizona, and to be certain that all forest series were adequately sampled to provide continuity with the earlier studies. In addition to habitat type descriptions, this paper includes a key to identify habitat types in the field.

STUDY AREA

The study area was restricted to the Douglas-fir zone in northern Arizona, which lies almost entirely within the Colorado Plateau Province (Wilson 1962). Most Douglas-fir stands in northern Arizona are within the boundaries of the Coconino, Kaibab, and Apache-Sitgreaves National Forests (fig. 1). Distribution of sampled stands by National Forest and Ranger District is shown in table 1.

Sampled stands exhibited a wide variety of site characteristics, growing at elevations ranging from 6,580 to 9,600 feet (2,005 to 2,925 m), on slopes ranging from 5% to 72%, and on all aspects. Soils were equally variable, having been developed from such diverse parent materials as andesite, basalt, and limestone.

²Nomenclature follows Lehr (1978) unless otherwise noted. A complete list of species encountered in this study can be found in Appendix B.

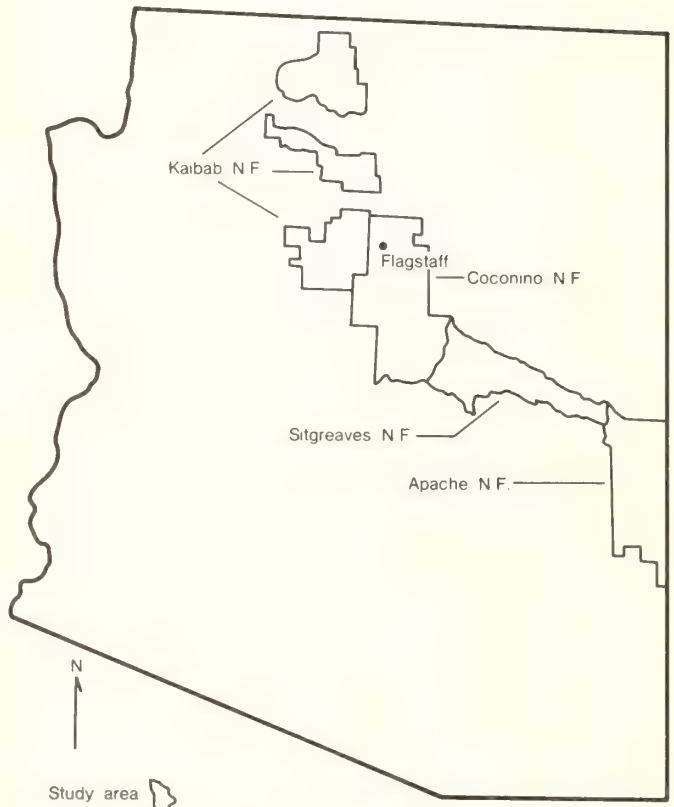


Figure 1.—National Forest boundaries encompassing study area within northern Arizona.

Although data were not collected, climatological conditions associated with the stands also were probably quite diverse. Extrapolating from climatological studies of ponderosa pine types in central Arizona by Beschta (1976), it appears that the Douglas-fir zone receives more than 25 inches of mean annual precipitation and has an average snowfall depth greater than 75 inches.

Table 1.—Douglas-fir plot locations by National Forest and Ranger District

National Forest	Ranger District	Number of plots
Kaibab	North Kaibab	10
	Chalender	5
	Williams	1
Coconino	Elden	9
	Blue Ridge	3
	Fort Valley	1
	Clifton	5
Apache-Sitgreaves	Alpine	9
	Springerville	3

METHODS

Field Sampling

Field sampling followed the procedures described by Pfister and Arno (1980). Sample stands were selected using the following criteria: (1) Douglas-fir dominated the stand or was a codominant species; (2) if it was a codominant, it exhibited as many or more stems in younger size classes as that shown by other codominants; (3) the stand was relatively undisturbed and mature, containing relatively old individual trees; and (4) the stand obviously was not an ecotone between other habitat types. Although Douglas-fir forests cover a relatively small geographical area, they are still subject to disturbances common to other forest types, especially those from timber harvesting and grazing by domestic livestock. Such areas were excluded from sampling in order to more accurately describe undisturbed conditions. Logged areas were quite obvious, whereas determining excessive grazing use required more careful observation regarding the presence of indicator species and recent soil disturbances.

An attempt was made to sample the entire range of site conditions that might support a Douglas-fir potential climax community, utilizing input from USDA Forest Service personnel to locate possible sample stands. Stands where *Abies concolor* was the dominant timber species, either in the overstory canopy or in regeneration size classes, were not sampled.

Once a stand was selected, a 375-m² circular plot was established in what appeared to be a relatively homogeneous and representative portion of the stand. Each plot center was permanently marked with an aluminum stake to facilitate relocation. Plot locations were identified on 1/2-inch scale National Forest maps and on topographic quadrangles, and were described by physiographic province, National Forest, Ranger District, locality, and legal description.³

Plots were described by elevation, slope, aspect, landform, parent material, and surface soil characteristics. Also included was the percentage of the plot surface covered by rocks, mosses, vascular plants, and litter. Notes were made regarding evidence of past fire, logging or grazing activity, and adjacent plant communities.

Vegetation in the plots was described in detail. The number of trees 2 inches or larger in diameter at breast height (d.b.h.) was recorded by species in 2-inch diameter size classes. Number of stems in two reproductive classes—(1) seedlings between 0.5 and 4.5 feet in height, and (2) saplings taller than 4.5 feet but less than 2 inches d.b.h.—was also recorded by species. At each plot center, basal area for the stand was sampled using a 10-factor prism to clarify stand structure; data were not used for estimating productivity.

Shrubs, forbs, and graminoids were recorded by species and percentage of plot area covered. The reliability of cover estimates was checked in the first plot, and in every tenth plot thereafter, by recording percentage

cover in 50 systematically placed, 20- × 50-cm quadrats within a 15- × 25-m, rectangular plot, overlying the original circular plot (Daubenmire and Daubenmire 1968). The percentage cover of an individual species within each quadrat was recorded by coverage class as outlined in Daubenmire (1968). Any species found in the stand, but not in a plot, was simply noted as present in the stand.

Data Analysis

As with field sampling, data analysis followed guidelines suggested by Pfister and Arno (1980). After all data were computer coded, subjective groupings of stands were made on the basis of similarity between vegetation composition and structure of the stands. Stands were then organized into a synthesis table consisting of species (rows) and stands (columns). By rearranging the order of stands into different groupings, the aggregation of stands could be compared, and if necessary, constantly refined by further rearrangement.

Once groupings appeared satisfactory, as judged by greater similarity of vegetation within than between groups, a principal component analysis (PCA) of the data was made. PCA ordines stands on abstract axes, positioning them, relative to one another, on the basis of similarity of percentage cover of individual species (Nichols 1977). Then, by comparing distribution of stands from the PCA to the subjective groupings, the validity of the latter could be verified more easily. If a stand appeared to be misgrouped as a result of the comparison, it was placed into a more appropriate group, or a new group was defined. Any changes made because of ordination were then incorporated into a new synthesis table. Throughout these procedures, continual reference was made to detailed field forms containing information on abiotic factors and observations to better explain vegetational relationships defined during analysis.

This procedure—continued refinement of groupings through synthesis table construction followed by PCA analysis—was repeated until individual groups were judged to represent a habitat type (h.t.). Furthermore, site characteristics, such as abiotic factors and histories of plot disturbances, were compared to maintain greater consistency within groups. According to Pfister and Arno (1980), such an iterative approach of successive approximations is central to the development of a habitat type classification.

Once habitat types were defined, vegetation and environmental data were synthesized to provide descriptions of the habitat types and to determine important indicator species. Finally, a key was developed to help the user determine the habitat type of sites in the Douglas-fir series within the study area.

RESULTS AND DISCUSSION

The four Douglas-fir habitat types of northern Arizona defined in this study are listed in table 2. In the following section, these habitat types are described with

³Data on file at the Rocky Mountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Flagstaff, Ariz.

Table 2.—Douglas-fir habitat types of northern Arizona, including name, abbreviation of the type and number of plots sampled in the type

Habitat type	Abbreviation	No. plots
<i>Pseudotsuga menziesii</i>	PSME/MUVI h.t.	9
<i>Muhlenbergia virescens</i>		
<i>Pseudotsuga menziesii</i> / <i>Festuca arizonica</i>	PSME/FEAR h.t.	6
<i>Pseudotsuga menziesii</i> / <i>Quercus gambelii</i>	PSME/QUGA h.t.	10
<i>Muhlenbergia virescens</i> phase	MUVI phase	1
<i>Pseudotsuga menziesii</i> /Sparse undergrowth	PSME/SPARSE h.t.	11
North Kaibab phase	N.K. phase	9

respect to diagnostic vegetation, topography, and ecotones and adjacent habitats. A brief discussion of each habitat type also is included.

A key to identify forest series and Douglas-fir stands by habitat types is presented in Appendix A. A plant list of all species found in sampled stands is shown in Appendix B. The average density and constancy (percentage occurrence within plots sampled) of trees and average cover and constancy of shrubs, graminoids, and forbs are listed in Appendix C.

Although the habitat type key is easy to apply, it has limitations that users must consider. First, the key is designed to be used in relatively undisturbed stands, because successional patterns leading to most habitat types are not yet well understood. Second, the key is intended for stands where Douglas-fir apparently will be the dominant tree species of the climax association, reproducing well enough to ensure its continued position in the stand. In situations where there is some doubt that Douglas-fir will be a prominent component of the climax community, users should consult references relating to habitat types of adjacent forest series, particularly Moir and Ludwig (1979) for spruce-fir and mixed conifer forests and Hanks et al. (1983) for the ponderosa pine series. Third, after the key has led to selection of a particular habitat type, compare the observed stand characteristics with the general description of the habitat type to see how well the stand fits the description. If the stand does not fit the description very well, try the key again, because it is only an identification aid and should always be used in conjunction with habitat type descriptions.

Pseudotsuga Menziesii/*Muhlenbergia Virescens* H.T. (PSME/MUVI; Douglas-fir/Screwleaf Muhly)

Diagnostic Vegetation

Pseudotsuga menziesii, the dominant timber species of this habitat type (fig. 2), regenerates well at all stand ages. *Abies concolor* is only accidental or rare, being represented best in the younger age classes. *Pinus ponderosa*, although low in density, is represented equally throughout the various size classes; its abun-



Figure 2.—*Pseudotsuga menziesii*/*Muhlenbergia virescens* habitat type. Plot 037, Horse Springs, Apache National Forest (8,280 feet or 2,525 m). This stand has good representation of *Pseudotsuga menziesii* in all size classes, with grass cover of *Muhlenbergia virescens* and low shrub cover.

dance, however, is reduced in stands approaching climax conditions. *Pinus strobiformis* also is present in small amounts, but is a prominent component of old stands. However, it is neither as abundant nor as dominant as *Pseudotsuga menziesii*.

Characteristically, the PSME/MUVI h.t. lacks a well-defined shrub layer. *Quercus gambelii* occurs only in trace amounts when found at all; it usually is absent. *Berberis repens*, *Pachystima myrsinites*, and *Symphoricarpos oreophilus* are all noticeably absent from samples of this type.

In marked contrast to shrubs, the grass component of this habitat type is well developed. Coverage of *Muhlenbergia virescens*, the diagnostic indicator species of this habitat type, varies from trace amounts to as much as 15%. While *Festuca arizonica* may be present in this type, it is minor with lower coverage values. Although *Koeleria pyramidata* (K. *cristata*)⁴ can be found on most sites throughout the type, it is not a good indicator, because it often is found in other types as well. *Bromus richardsonii*, *Carex rossii*, *Sitanion hystrix*, and *Poa fendleriana* are all common elements of this habitat type.

Within the forb component, *Dugaldia hoopesii* (*Helenium hoopesii*) is a consistent species, and although never covering more than 1% of a plot, it usually can be found. *Lithospermum multiflorum*, *Geranium richardsonii*, and *Fragaria ovalis* also are common elements. Ubiquitous species which occur throughout this type include *Thalictrum fendleri* and *Pseudocymopterus montanus*.

⁴Scientific nomenclature follows Lehr (1978), which is most current. However, that of Kearney and Peebles (1960) is cited in parentheses where different from Lehr, because it is more commonly used in Arizona.

Topography

The PSME/MUVI h.t. was sampled between 7,800 and 8,700 feet (2,375 to 2,650 m) elevation. It is found primarily on northwest- to west-facing slopes, but occasionally occurs on south aspects as well. Generally, the PSME/MUVI h.t. is found on ridge sideslopes or on upper slopes of large canyons. The type has a well developed litter layer and low (less than 10%) rock coverage on the soil surface. This habitat type was sampled on basaltic parent material.

Ecotones and Adjacent Habitats

The PSME/MUVI h.t. is commonly found between wetter *Abies concolor* habitat types and drier *Pinus ponderosa* habitat types. It often can be found on drier sides of ridges, with *Abies concolor* on wetter sides and ridge tops. Quite often, the transition into the PSME/MUVI h.t. is abrupt, signalling an equally abrupt environmental change. Typical *Pinus ponderosa* habitat types found at elevations below the PSME/MUVI h.t. are the PIPO/MUVI h.t. or the PIPO/MUVI-FEAR h.t. (Hanks et al. 1983).

Discussion

The PSME/MUVI h.t., a widespread and abundant type in the Douglas-fir series of the study area, is found in the Apache-Sitgreaves National Forest in the White Mountains. Although no stands were observed generally west of the White Mountains, the habitat type may occur near the western part of the Mogollon Rim, where site characteristics and environmental situations similar to those in the White Mountains can be found.

The area covered by individual stands of the PSME/MUVI h.t. is relatively small. However, extensive stands can be found in the Campbell River and Bear Creek areas, presumably because of the greater areal expanse of ridge sideslopes with environmental conditions favorable to support the PSME/MUVI h.t.

Moir and Ludwig (1979) recognize a *Pseudotsuga menziesii*-*Pinus strobiformis*/Muhlenbergia virescens habitat type. Evidence from this study supports their general description, but differs in that *Pinus strobiformis* is not recognized as a dominant climax species; Moir and Ludwig support this conclusion.⁵ Moir and Ludwig (1979) also indicate that this habitat type is located on south and west aspects, whereas in this study, many plots were found on northwest and east aspects.

Because of the inherent susceptibility of young Douglas-fir to surface fires, the PSME/MUVI h.t. probably is greatly influenced by fire. Frequent fires of low intensity would likely favor *Muhlenbergia virescens* and would reduce the number of trees growing into the overstory. Whether the overstory composition would change from *Pseudotsuga menziesii* to *Pinus ponderosa*, however, is questionable. Although some stands in this habitat type contained old, fire-scarred *Pinus ponderosa*,

⁵Personal communication with William H. Moir, USDA Forest Service, Southwestern Region, Albuquerque, N. Mex., 1982.

others showed little or no evidence of fire; but *P. ponderosa* was still present.

Pseudotsuga Menziesii/*Festuca Arizonica* H.T. (PSME/FEAR; Douglas-fir/Arizona Fescue)

Diagnostic Vegetation

Pseudotsuga menziesii is the dominant climax tree species in the PSME/FEAR h.t. (fig. 3), and regeneration is often moderate to heavy under an old-growth canopy. *Abies concolor* is absent from this habitat type, while *Pinus ponderosa* maintains itself under the *Pseudotsuga menziesii* canopy, but always in a subclimax or successional status. *Pinus strobiformis* is a minor climax species, but never attains the status of *Pseudotsuga menziesii*. At higher elevations within this habitat type, *Pinus ponderosa* may be absent.

There is essentially no representation of a shrub layer in this habitat type, except for *Berberis repens*, with an average cover of about 4% for stands sampled in this study.

The grass component is well developed, with as much as 10% to 15% of a given plot covered by grass. *Festuca arizonica* occurs in all stands, and is a diagnostic feature for identifying this habitat type. *Muhlenbergia montana* is nearly as constant and abundant as *Festuca arizonica*, but is much more ubiquitous, occurring throughout a variety of habitat types. *Poa fendleriana* also is constant in this habitat type, but is so ubiquitous as to be of little use as an indicator species. Other common graminoid species include *Bromus richardsonii*, *Carex rossii*, and *Sitanion hystrix*.

Species constituting the forb layer of the PSME/FEAR h.t. show low constancy values. Forbs that are common, but not restricted to this habitat type, include *Antennaria parvifolia*, *Lithospermum multiflorum*, *Penstemon barbatus*, and *Pseudocymopterus montanus*. Percent coverage of *Valeriana capitata* (*V. acutiloba*) is occasionally high, but the species is often absent.

Topography

The elevational range of the PSME/FEAR h.t. is wide. It can be found as low as 6,800 feet (2,075 m) and as high as 9,500 feet (2,895 m), but most commonly occurs near 8,500 feet (2,590 m). The PSME/FEAR h.t. can be found on ridge sideslopes and occasionally in canyons on upper slopes, usually on east or northeast exposures. A relatively high percentage of mineral soil and rock is exposed in this type. Fifteen percent of a plot may be bare ground and rock, which is consistently higher than in other *Pseudotsuga menziesii* types. Andesite and basalt were common parent materials found at sites of this habitat type.

Ecotones and Adjacent Habitats

The PSME/FEAR h.t. often occurs where, because of topography, the transitional zone from *Pinus ponderosa*

to *Abies concolor* habitat types is rather gradual. The PSME/FEAR h.t. commonly is found on upland sites, away from the Mogollon Rim. A typical habitat type in the adjacent *Pinus ponderosa* series is *Pinus ponderosa*/*Festuca arizonica*, while the *Abies concolor*/*Festuca arizonica* habitat type is representative of the adjacent *Abies concolor* series.

Discussion

The PSME/FEAR h.t. is found throughout the Coconino and Kaibab National Forests, in the vicinity of the San Francisco Peaks, except the area east of the Blue Ridge Ranger District of the Coconino. However, it may well occur on the Chevelon Ranger District of the Apache-Sitgreaves National Forest, because the area exhibits environmental conditions that appear similar to other locations where the type is found.

On the Coconino National Forest, this habitat type was found to occupy more area than other habitat types in the *Pseudotsuga menziesii* series. As with the PSME/MUVI h.t., the PSME/FEAR h.t. is greatly influenced by fire. With very frequent fires, *Festuca arizonica* would increase in abundance, while canopy densities would probably be reduced. Similar to the PSME/MUVI h.t., many plots had no old, fire-scarred *Pinus ponderosa* upon which to base past fire history. As a consequence, the question again arises as to whether *Pseudotsuga menziesii* would be dominant under a frequent fire regime.

Pseudotsuga Menziesii/*Quercus Gambelii* H.T. (PSME/QUGA; Douglas-fir/Gambel Oak)

Diagnostic Vegetation

Pseudotsuga menziesii is the climax dominant tree species in the PSME/QUGA h.t. (fig. 4). Even though the



Figure 3.—*Pseudotsuga menziesii*/*Festuca arizonica* habitat type. Plot 044, San Francisco peaks, Coconino National Forest (8,600 feet or 2,620 m). *Festuca arizonica* is the dominant grass species; shrub cover is low under a relatively open canopy.



Figure 4.—*Pseudotsuga menziesii*/*Quercus gambelii* habitat type. Plot 023, East Eagle Creek, Apache National Forest (7,520 feet or 2,290 m). The canopy on these sites is often open, with *Pinus ponderosa* present. *Quercus gambelii* is prominent and percent grass cover is low.

canopy in seral stands may be composed of other tree species, *Pseudotsuga menziesii* is the dominant class of regeneration. *Abies concolor* may be present in this habitat type as a minor timber species, but it does not attain dominant status. In instances where regeneration of *Abies concolor* is present, that of *Pseudotsuga menziesii* will still be found in far greater numbers. Although *Pinus strobus* and *Pinus ponderosa* can occur in all age classes, both are minor climax species in older stands. On sites dominated by old individuals of *Pseudotsuga menziesii*, *Pinus strobus* will have a greater density than *Pinus ponderosa*.

Gambel oak (*Quercus gambelii*) in the area covered by this habitat type classification was observed only in shrub form, in contrast to *Pinus ponderosa* habitat types developed by Hanks et al. (1983), in which Gambel oak reached tree size. As indicated by the habitat type name, the shrub layer is dominated by *Q. gambelii*, which can cover as much as 70% of a plot. Under conditions where canopy coverage by Gambel oak is high, the density of the mature timber overstory is greatly reduced, apparently because of competition from the Gambel oak undergrowth. Conifer regeneration in the understorey, however, may still be high. *Berberis repens*, *Pachystima myrsinites*, *Robinia neomexicana*, and *Symphoricarpos oreophilus* are common.

Poa fendleriana is common, but *Bromus richardsonii* and *Carex rossii* contribute the largest percentage of grass or grasslike cover. The latter species, while most constant, are not diagnostic because of their ubiquity in other habitat types of the *Pseudotsuga menziesii* series. Small amounts of *Muhlenbergia virescens* also may occur, but overall, the graminoid component of the typic phase is not well developed.

There is little consistency in the forb component of this habitat type. *Dugaldia hoopesii* (*Helenium hoopesii*), *Lathyrus arizonicus*, *Pseudocymopterus montanus*, *Pter-*

idium aquilinum, and *Thalictrum fendleri* are all common elements of the undergrowth.

Muhlenbergia virescens phase.—The MUVI phase of the PSME/QUGA h.t. differs from the typic phase in that the graminoid component is well developed. *Muhlenbergia virescens* will dominate the herbaceous undergrowth, with coverage values as high as 15%. *Bromus richardsonii*, *Carex rossii*, *Poa fendleriana*, and *Sitanion hystrix* are all common components, whereas *Festuca arizonica* and *Muhlenbergia montana* are absent.

Topography

The elevational range of the PSME/QUGA h.t. is variable. It is most prominent between 6,900 and 7,700 feet (2,105 and 2,345 m), but sites up to 9,000 feet (2,745 m) are not uncommon. Generally, the habitat type is found in canyons, at mid-slope. The ground surface of the PSME/QUGA h.t. can be quite rocky, reaching 20% coverage. The litter layer, however, is still well developed.

The MUVI phase can be found between 7,500 and 9,000 feet (2,285 and 2,745 m) on ridges situated at lower to middle slopes. It can occur on all aspects, with the south and southwest aspects most common. Soils can vary, often being thin and rocky.

Ecotones and Adjacent Habitats

The PSME/QUGA h.t. is often the lowest elevational representative of the *Pseudotsuga menziesii* series. It occurs on sites which are moist enough to support establishment of *P. menziesii*, generally protected drainages or canyons, where *Abies concolor* apparently becomes drought-stressed. Such differential moisture requirements result in abrupt transitions between adjoining habitat types, often related to microsite differences associated with sharp topographical changes.

Small stands of this habitat type can be found in steep drainages in the Mogollon Rim area. These stands are often adjacent to moist *Abies concolor* habitat types in drainage bottoms, probably the ABCO/QUGA h.t. Upslope from the PSME/QUGA h.t. in such drainages, the habitat type generally found is *Pinus ponderosa*/*Quercus gambelii*.

When the habitat type occurs on well-drained upland sites, generally as the MUVI phase, it is found between the drier *Pinus ponderosa*/*Muhlenbergia virescens* habitat type (Hanks et al. 1983) at lower elevations, and the *Abies concolor*/*Quercus gambelii* habitat type, *Muhlenbergia virescens* phase, at higher cooler sites. The MUVI phase of the PSME/QUGA h.t. bridges grass-dominated *Pinus ponderosa* habitat types and shrub-dominated *Abies concolor* habitat types.

Discussion

The PSME/QUGA h.t. is common on the Apache-Sitgreaves, Coconino, and Kaibab National Forests. It is

located most frequently along the Mogollon Rim, in canyons dissecting the Rim. The habitat type can also be found along the eastern rim of the North Kaibab Plateau as it descends into the Colorado River Drainage.

Locally, the PSME/QUGA h.t. is very limited—so narrow in some areas that it can be considered only as an ecotone between the lower (warmer) pine forests and the higher (cooler) mixed conifer forests. In other areas, it may be lacking entirely.

Although only one plot representing the MUVI phase was sampled in this study, comparison with ongoing studies on the Gila National Forest,⁶ where the MUVI phase of the PSME/QUGA h.t. is well documented, suggests that the sample plot was properly classified. It is believed that the phase is common on the Alpine and Clifton Ranger Districts of the Apache-Sitgreaves National Forest.

Pseudotsuga menziesii/Sparse Undergrowth H.T. (PSME/SPARSE; Douglas-fir/Sparse Undergrowth)

Diagnostic Vegetation

Pseudotsuga menziesii is the dominant climax tree species in this habitat type (fig. 5), and its regeneration is sometimes quite heavy. *Abies concolor* often can be found on these sites as a minor component. Sites with greater than accidental *Abies concolor* representation, particularly in the regeneration classes, are ecotonal to *Abies concolor* habitat types. The relative abundance of *Pinus strobiformis* and *P. ponderosa* is a function of moisture; on wetter sites, *P. strobiformis* will be more abundant, while *P. ponderosa* will be more common on drier sites. Both pines are consistently found, but play a very minor part in the climax overstory.

The most diagnostic feature of the habitat type is the lack of a substantial shrub, grass, and forb undergrowth, which is generally less than 10% of the total plot coverage. Other habitat types of the *Pseudotsuga menziesii* series have undergrowth coverages greater than 10% with at least one diagnostic species exceeding 1%. An opening in the canopy will result in an increase in regeneration of *P. menziesii*, while undergrowth species remain sparse.

Berberis repens is the only shrub species which frequently showed more than 1% coverage in the PSME/SPARSE h.t. It is not diagnostic, however, because constancy was low and distribution was widespread throughout the *Pseudotsuga menziesii* series.

On the Coconino and southern part of the Kaibab National Forests, *Festuca arizonica* often can be found in the habitat type, but never with greater than 1% coverage. *Bromus richardsonii* and *Poa fendleriana* also are common grasses of this habitat type. There is very little consistency among the forbs of this habitat type.

North Kaibab (N.K.) phase.—The North Kaibab phase (fig. 6) was segregated from the general PSME/SPARSE h.t., because it displayed some features on the North

⁶Personal communication with E. Lee Fitzhugh, Wildlife Extension, University of California, Davis, 1982.

Kaibab Plateau that were distinct from the southern counterpart of the habitat type. Primarily, the presence of *Clematis ligusticifolia* and *Valeriana capitata* (*V. acutiloba*) was common in the North Kaibab phase.

Pinus strobiformis was notably absent from this phase. *Berberis repens* is fairly constant, with coverage values greater than 1%, and *Pachystima myrsinites*, a small shrub component of this phase, is common. *Clematis ligusticifolia* and *Valeriana capitata* (*V. acutiloba*) are common species in the North Kaibab phase, although they rarely have coverage values greater than 1%. These two species are absent from the typic type of the Coconino and southern Kaibab National Forests.

Topography

The PSME/SPARSE h.t. ranges from 7,000 to 8,500 feet (2,135 to 2,590 m). In the Coconino and southern portion of the Kaibab National Forests, it can be found on ridges near mid-slope. On the Kaibab Plateau, it is found in canyons on lower slopes. Aspects generally range from east to northeast to north to northwest, but the North Kaibab phase is found strictly on north to northeast, and occasionally, northwest slopes.

Ecotones and Adjacent Habitats

In the Coconino and southern Kaibab National Forests, the PSME/SPARSE h.t. is transitional between the *Pinus ponderosa* grass and the *Abies concolor* shrub habitat types. Its presence may signify an environmental change that favors grass undergrowth rather than a closed canopy of shrubs. Changes from the lower *Pinus ponderosa* grass type to this PSME/SPARSE h.t. are usually abrupt; the canopy closes in, while the under-



Figure 5.—*Pseudotsuga menziesii*/Sparse undergrowth habitat type. Plot 001, Kendrick Peak, Kaibab National Forest (8,850 feet or 2,695 m). Canopy cover can be dense, with no representation of the shrub component, and low shrub diversity.



Figure 6.—*Pseudotsuga menziesii*/Sparse undergrowth habitat type, North Kaibab phase. Plot 007, Big Springs, Kaibab National Forest (7,500 feet or 2,285 m). Stands of this habitat type have a dense canopy, very little shrub representation and low forb cover. *Pinus strobiformis* is absent from these stands. This habitat type occurs only on the North Kaibab Plateau.

growth vegetation practically disappears. The near absence of undergrowth vegetation cannot be attributed to any disturbance observed during the study.

On the North Kaibab Plateau, the PSME/SPARSE h.t. is typically found in canyons. Transitions from other types to the PSME/SPARSE h.t. are rather abrupt, except for the more gradual mergence with adjacent *Abies concolor* types. In some instances, transitional changes are correlated with gradual changes in aspect.

Discussion

The PSME/SPARSE h.t. is, perhaps, the most difficult of *Pseudotsuga menziesii* habitats to identify. It exists as a distinct habitat type based on the lack of a diagnostic undergrowth, and has little affinity with other types. Two phases are recognized: the typic phase occurs in the Coconino and southern Kaibab National Forests, and the North Kaibab phase is found on the North Kaibab Plateau, as indicated by its name. The phases are quite distinct from each other regarding key species and locality, but share the lack of an abundant shrub, grass, and forb undergrowth.

The PSME/SPARSE h.t. includes plots found on the north side of the San Francisco Peaks and on the south side of Kendrick Peak. These plots are found on stony soils originating from either basalt or andesite, and are noteworthy because of the presence of *Pseudotsuga menziesii* at high elevations—8,500 to 8,900 feet (2,590 to 2,715 m). *Abies concolor*, while expected in this habitat type following observation of other sites with similar aspects and elevations, is noticeably absent, perhaps as a result of the well-drained nature of the soils, creating drier site conditions. The PSME/SPARSE h.t. may denote a warmer site that is similar to Moir and Ludwig's (1979) *Abies concolor*-*Pseudotsuga menziesii* (SPARSE) habitat type, but the relationship is not clear.

CONCLUSIONS

These descriptions may have to be modified somewhat as more stands are encountered and knowledge of each habitat type increases. However, each of the habitat types described in this paper are believed to be distinct, recognizable units in the environment.

The study denotes only the first stage in classification—the identification of habitat types. For such a classification to be most useful, additional information is needed on successional relationships within habitat types and on the response of habitat types to various types of treatment. This information can best be gained through the cooperative efforts of forest managers and forest researchers.

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APPENDIXES

Appendix A. Keys to the Series Level and Habitat Types for *Pseudotsuga menziesii* of Northern Arizona¹

Key to Series

- | | |
|--|---|
| 1. <i>Abies concolor</i> present, not accidental or seral | <i>Abies concolor</i> series
(Moir and Ludwig 1979) |
| 1. <i>Abies concolor</i> absent, or accidental | 2 |
| 2. <i>Pseudotsuga menziesii</i> dominant, <i>Pinus ponderosa</i> codominant or seral | <i>Pseudotsuga menziesii</i> series
(see habitat type key) |
| 2. <i>Pseudotsuga menziesii</i> absent or accidental, <i>Pinus ponderosa</i> dominant, clearly not seral | <i>Pinus ponderosa</i> series
(Hanks et al. 1983) |

Key to Habitat Types

- | | |
|--|----------------------------|
| 1. <i>Quercus gambelii</i> well represented (greater than 5% cover) | 2 |
| 1. <i>Quercus gambelii</i> not well represented (less than 5% cover) | 3 |
| 2. <i>Muhlenbergia virescens</i> common (greater than 1% cover) | PSME/QUGA
MUVI PHASE |
| 2. <i>Muhlenbergia virescens</i> scarce (less than 1% cover) | PSME/QUGA
TYPIC PHASE |
| 3. <i>Muhlenbergia virescens</i> present; <i>Festuca arizonica</i> absent or minor | PSME/MUVI |
| 3. <i>Muhlenbergia virescens</i> absent or minor | 4 |
| 4. <i>Festuca arizonica</i> common (greater than 1% cover) | PSME/FEAR |
| 4. <i>Festuca arizonica</i> scarce (not over 1% cover); undergrowth never greater than 10% cover | 5 |
| 5. Undergrowth sparse (less than 10% cover); Coconino and southern Kaibab National Forests | PSME/SPARSE
TYPIC PHASE |
| 5. Undergrowth sparse (less than 10% cover), <i>Clematis ligusticifolia</i> and <i>Valeriana capitata</i> common; North Kaibab Plateau | PSME/SPARSE
N.K. PHASE |

¹Percent canopy coverage values used in this key were derived from field data which were collected from 375-m² circular plots.

Appendix B. Plant List from Sampled *Pseudotsuga menziesii* Stands in Northern Arizona

I. Trees

Abies concolor
Abies lasiocarpa
Juniperus scopulorum
Picea engelmannii
Pinus edulis
Pinus ponderosa
Pinus strobiformis
Populus tremuloides
Pseudotsuga menziesii

ABCO¹
 ABLA
 JUSC
 PIEN
 PIED
 PIPO
 PIST
 POTR
 PSME

II. Shrubs

Amelanchier utahensis
Berberis repens
Brickellia californica
Ceanothus fendleri
Holodiscus dumosus
Juniperus communis
Lonicera spp.
Lonicera involucrata
Pachystima myrsinites
Prunus spp.
Prunus virginiana
Quercus gambelii
Rhamnus californica
Ribes spp.
Ribes aureum
Robinia neomexicana
Rosa arizonica
Rubus strigosus
Sambucus glauca
Symphoricarpos oreophilus
Vaccinium oreophilum

AMUT
 BERE
 BRCA
 CEFE
 HODU
 JUCO
 LONICE
 LOIN
 PAMY
 PRUNUS
 PRVI
 QUGA
 RHCA
 RIBES
 RIAU
 RONE
 ROAR
 RUST
 SAGL
 SYOR
 VAOR

III. Graminoids

Bromus richardsonii
Carex spp.
Carex rossii
Cyperus spp.
Festuca arizonica
Koeleria pyramidata (*Koeleria cristata*)
Luzula parviflora
Melica porteri
Muhlenbergia spp.
Muhlenbergia montana
Muhlenbergia virescens
Oryzopsis micrantha
Poa fendleriana
Schizachyrium scoparium
 (Andropogon scoparius)
Sitanion hystrix

BRRI
 CAREX
 CARO
 CYPERU
 FEAR
 KOPY
 LUPA
 MEPO
 MUHLEN
 MUMO
 MUVI
 ORMI
 POFE
 SCSC
 SIHY

IV. Forbs

Achillea millefolium (*Achillea lanulosa*)
Antennaria marginata
Antennaria parvifolia
Aquilegia spp.
Aquilegia chrysantha
Aquilegia elegantula
Arabis fendleri
Arenaria spp.
Arenaria eastwoodiae
Artemisia carruthii
Artemisia dracunculus (*A. dracunculoides*)
Artemisia ludoviciana
Aster foliaceus
Astragalus spp.
Astragalus rusbyi
Castilleja integra
Chaptalia alsophila
Chimaphila umbellata
Cirsium parryi
Clematis ligusticifolia
Corallorhiza striata
Cryptantha jamesii
Cystopteris fragilis
Disporum trachycarpum
Dugaldia hoopesii (*Helenium hoopesii*)
Erigeron spp.
Erigeron divergens
Erigeron macranthus
Erigeron platyphyllus
Erigeron superbus
Eriogonum jamesii
Eriogonum racemosum
Euphorbia lurida
Fragaria bracteata
Fragaria ovalis
Galium spp.
Galium boreale
Galium mexicanum (*Galium asperrimum*)
Geranium caespitosum
Geranium richardsoni
Heuchera parviflora
Heuchera rubescens
Hieracium fendleri
Hymenoxys richardsonii
Ipomoea spp.
Ipomopsis aggregata (*Gilia aggregata*)
Ipomopsis multiflora (*Gilia multiflora*)
Lathyrus arizonicus
Lithospermum multiflorum
Lotus wrightii
Lupinus argenteus
Malaxis soulei

ACMI
 ANMA
 ANPA
 AQUELE
 AQCH
 AQEL
 ARFE
 ARENAR
 AREA
 ARCA
 ARDR
 ARLU
 ASFO
 ASTRAG
 ASRU
 CAIN
 CHAL
 CHUM
 CIPA
 CLLI
 COST
 CRJA
 CYFR
 DITR
 DUHO
 ERIGER
 ERDI
 ERMA
 ERPL
 ERSU
 ERJA
 ERRA
 EULU
 FRBR
 FROV
 GALIUM
 GABO
 GAME
 GECA
 GERI
 HEPA
 HERU
 HIFE
 HYRI
 IPOMOE
 IPAG
 IPMU
 LAAR
 LIMU
 LOWR
 LUAR
 MASO

Appendix B.—(Continued)

<i>Mirabilis oxybaphoides</i>	MIOX	<i>Rhus radicans</i>	RHRA
<i>Monotropa</i> spp.	MONOTR	<i>Sedum</i> spp.	SEDUM
<i>Monotropa latisquama</i>	MOLA	<i>Senecio bigelovii</i>	SEBI
Mustard spp. (Cruciferae family)	MUSTAR	<i>Senecio eremophilus</i> (<i>Senecio macdougalii</i>)	SEER
Orchid spp. (Orchidaceae family)	ORCHID	<i>Senecio neomexicanus</i>	SENE
<i>Osmorhiza chilensis</i>	OSCH	<i>Silene laciniata</i>	SILA
<i>Osmorhiza depauperata</i>	OSDE	<i>Silene scouleri</i>	SISC
<i>Oxalis alpina</i> (<i>Oxalis metcalfei</i>)	OXAL	<i>Smilacina racemosa</i>	SMRA
<i>Oxytropis lambertii</i>	OXLA	<i>Smilacina stellata</i>	SMST
<i>Penstemon</i> spp.	PENSTE	<i>Solidago decumbens</i>	SODE
<i>Penstemon barbatus</i>	PEBA	<i>Solidago sparsiflora</i>	SOSP
<i>Penstemon virgatus</i>	PEVI	<i>Stellaria jamesiana</i>	STJA
<i>Petrophytum caespitosum</i>	PECA	<i>Swertia radiata</i>	SWRA
<i>Phaseolus parvulus</i>	PHPA	<i>Thalictrum fendleri</i>	THFE
<i>Polemonium foliosissimum</i>	POFO	<i>Thermopsis pinetorum</i>	THPI
<i>Potentilla crinita</i>	POCR	<i>Thlaspi</i> spp.	THLASP
<i>Potentilla norvegica</i>	PONO	<i>Valeriana capitata</i> (<i>V. acutiloba</i>)	VACA
<i>Potentilla thurberi</i>	POTH	<i>Vicia</i> spp.	VICIA
<i>Pseudocymopterus montanus</i>	PSMO	<i>Vicia americana</i>	VIAM
<i>Pteridium aquilinum</i>	PTAQ	<i>Vicia pulchella</i>	VIPU
<i>Pterospora andromeda</i>	PTAN	<i>Viola</i> spp.	VIOLA
<i>Pyrola secunda</i>	PYSE	<i>Viola canadensis</i>	VICA

¹Four letter acronyms were formed from the first two letters of the generic name and the first two letters of the specific name. In those cases where an individual was only identified to genus, a six-letter acronym was assigned using the first six letters of the generic name (or a five letter acronym was used if the generic name contained only five letters).

Appendix C. Table of Average Cover and Constancy of Major Species by *Pseudotsuga menziesii* Habitat Types in Northern Arizona¹

Species	PSME/QUGA		PSME/MUVI (N = 9)	PSME/FEAR (N = 6)	PSME/SPARSE	
	MUVI Phase (N = 1)	Typic Phase (N = 10)			Typic Phase (N = 11)	N.K. Phase (N = 9)
Trees						
<i>Abies concolor</i> < 4.5 ft	.	4.2/60	1.3/44	.	20.0/36	33.5/22
<i>A. concolor</i> > 4.5 ft and < 2 inch d.b.h.	.	2.5/20	1.5/22	2.0/17	2.5/18	10.0/11
<i>A. concolor</i> 2-4 inch d.b.h.	.	3.5/70	1.3/44	1.0/17	2.0/9	1.0/11
<i>A. concolor</i> 4-6 inch d.b.h.	.	4.0/50	1.0/11	2.0/17	3.0/9	.
<i>A. concolor</i> 6-8 inch d.b.h.	.	2.0/20	1.0/11	1.0/17	.	1.0/22
<i>A. concolor</i> 8-10 inch d.b.h.	.	1.5/30	.	.	1.0/9	.
<i>A. concolor</i> 10-12 inch d.b.h.	.	1.0/30	.	.	1.0/9	.
<i>A. concolor</i> 12-14 inch d.b.h.
<i>A. concolor</i> 16-18 inch d.b.h.	1.0/11
<i>A. concolor</i> 18-20 inch d.b.h.
<i>A. concolor</i> 20-22 inch d.b.h.
<i>A. concolor</i> > 22 inch d.b.h.	1.0/9	.
<i>Pinus ponderosa</i> < 4.5 ft	1.0/100	1.6/30	1.8/44	6.5/67	1.5/18	2.0/11
<i>P. ponderosa</i> > 4.5 ft and < 2 inch d.b.h.	1.0/100	2.0/30	2.0/44	6.0/17	5.3/36	1.0/11
<i>P. ponderosa</i> 2-4 inch d.b.h.	4.0/100	1.4/50	5.3/44	2.3/50	3.8/45	3.0/22
<i>P. ponderosa</i> 4-6 inch d.b.h.	6.0/100	2.0/50	3.3/67	1.8/67	2.0/54	2.3/44
<i>P. ponderosa</i> 6-8 inch d.b.h.	.	1.5/60	1.3/44	1.0/17	2.8/45	1.5/44
<i>P. ponderosa</i> 8-10 inch d.b.h.	.	1.5/40	1.4/56	1.5/33	2.5/54	1.2/55
<i>P. ponderosa</i> 10-12 inch d.b.h.	.	2.5/20	1.8/56	3.0/17	1.0/36	1.8/44
<i>P. ponderosa</i> 12-14 inch d.b.h.	.	1.0/10	1.0/33	1.5/33	1.0/18	1.0/33
<i>P. ponderosa</i> 14-16 inch d.b.h.	.	2.0/10	1.2/56	1.0/33	1.0/9	1.3/44
<i>P. ponderosa</i> 16-18 inch d.b.h.	.	2.0/10	1.0/22	1.5/33	1.0/36	1.5/22
<i>P. ponderosa</i> 18-20 inch d.b.h.	.	1.0/10	1.3/33	1.0/17	1.0/18	1.0/33
<i>P. ponderosa</i> 20-22 inch d.b.h.	.	1.0/20	1.0/22	1.0/17	1.0/9	.
<i>P. ponderosa</i> > 22 inch d.b.h.	.	1.0/10	1.0/22	1.0/17	1.0/9	1.5/44
<i>Pinus strobiformis</i> < 4.5 ft	1.0/100	2.2/50	1.2/67	5.2/83	4.8/73	.
<i>P. strobiformis</i> > 4.5 ft and < 2 inch d.b.h.	6.0/100	1.2/40	2.3/44	2.5/67	5.0/36	.
<i>P. strobiformis</i> 2-4 inch d.b.h.	.	1.4/50	2.2/56	4.2/83	3.8/45	.
<i>P. strobiformis</i> 4-6 inch d.b.h.	.	1.5/40	2.2/56	4.6/50	4.5/36	.
<i>P. strobiformis</i> 6-8 inch d.b.h.	.	1.2/40	2.0/33	1.6/50	2.3/36	.
<i>P. strobiformis</i> 8-10 inch d.b.h.	1.0/100	1.0/10	1.6/33	2.5/33	2.6/27	.
<i>P. strobiformis</i> 10-12 inch d.b.h.	.	1.0/10	1.3/44	1.5/33	1.7/27	.
<i>P. strobiformis</i> 12-14 inch d.b.h.	.	1.0/10	1.3/44	2.0/17	2.5/18	.
<i>P. strobiformis</i> 14-16 inch d.b.h.	1.0/100	.	.	1.0/17	1.0/9	.
<i>P. strobiformis</i> 16-18 inch d.b.h.	.	1.0/10	.	2.0/33	1.0/9	.
<i>P. strobiformis</i> 18-20 inch d.b.h.	1.0/27	.
<i>P. strobiformis</i> 20-22 inch d.b.h.	.	.	.	1.0/17	1.0/18	.
<i>P. strobiformis</i> > 22 inch d.b.h.	.	1.0/10	1.0/11	1.0/17	1.7/27	.
<i>Pseudotsuga menziesii</i> < 4.5 ft	5.0/100	24.8/90	11.2/100	10.0/100	31.2/91	12.8/77
<i>P. menziesii</i> > 4.5 ft and < 2 inch d.b.h.	4.0/100	11.6/80	13.7/100	5.0/83	21.8/73	13.8/55
<i>P. menziesii</i> 2-4 inch d.b.h.	3.0/100	9.8/100	12.0/89	6.2/100	16.5/91	8.9/77
<i>P. menziesii</i> 4-6 inch d.b.h.	4.0/100	4.0/70	2.9/89	9.0/50	4.8/91	6.1/77
<i>P. menziesii</i> 6-8 inch d.b.h.	.	3.6/60	5.4/56	4.5/33	4.1/91	3.4/77
<i>P. menziesii</i> 8-10 inch d.b.h.	.	2.4/50	3.0/78	2.6/50	4.0/82	1.4/51
<i>P. menziesii</i> 10-12 inch d.b.h.	.	3.0/40	2.6/67	2.0/33	2.0/82	3.4/55
<i>P. menziesii</i> 12-14 inch d.b.h.	1.0/100	1.0/30	1.6/56	1.5/33	1.5/54	2.0/44
<i>P. menziesii</i> 14-16 inch d.b.h.	2.0/100	1.0/30	1.0/44	1.5/33	1.0/45	1.5/44
<i>P. menziesii</i> 16-18 inch d.b.h.	.	2.0/20	2.5/22	2.0/17	1.0/9	1.5/22
<i>P. menziesii</i> 18-20 inch d.b.h.	.	1.0/20	1.0/33	1.0/17	1.8/45	1.0/33
<i>P. menziesii</i> 20-22 inch d.b.h.	.	1.0/50	1.0/33	1.0/50	1.3/36	2.0/11
<i>P. menziesii</i> > 22 inch d.b.h.	.	3.0/50	2.0/67	1.5/33	1.0/45	1.6/33
Shrubs						
<i>Amelanchier utahensis</i>	2.0/22
<i>Berberis repens</i>	.	1.3/20	.	3.8/83	1.8/73	2.1/89
<i>Ceanothus fendleri</i>	.	T/10	T/33	1.0/50	T/27	.
<i>Holodiscus dumosus</i>	.	.	.	2.0/17	2.0/9	.
<i>Lonicera involucrata</i>	.	1.0/10	.	.	.	1.0/22
<i>Pachystima myrsinites</i>	T/100	1.0/20	T/33	.	T/9	1.0/55
<i>Quercus gambelii</i>	40.0/100	22.0/100	T/22	T/17	1.0/9	1.7/55
<i>Robinia neomexicana</i>	6.0/100	1.5/50	2.0/11	3.0/17	1.0/9	T/55
<i>Symphoricarpos oreophilus</i>	2.0/100	4.5/30	.	1.0/17	T/54	4.1/55
<i>Vaccinium oreophilum</i>

Appendix C.—(Continued)

Graminoids

<i>Bromus richardsonii</i>	T/100	1.0/80	T/78	1.0/83	T/82	T/22
<i>Carex rossii</i>	1.0/100	1.0/80	1.0/78	1.0/67	T/36	T/33
<i>Festuca arizonica</i>	.	T/10	2.0/22	3.8/100	T/91	.
<i>Koeleria pyramidata</i>	.	T/30	T/100	2.0/17	T/18	T/44
<i>Muhlenbergia montana</i>	.	.	.	4.4/83	1.0/45	.
<i>Muhlenbergia virescens</i>	18.0/100	1.0/40	4.5/00	5.0/17	.	.
<i>Poa fendleriana</i>	T/100	1.0/70	T/55	1.3/100	T/54	1.0/100
<i>Sitanion hystrix</i>	T/100	T/30	T/55	1.0/50	T/18	T/11

Forbs

<i>Antennaria marginata</i>	.	T/10	T/11	.	.	.
<i>Antennaria parvifolia</i>	.	T/20	T/55	T/83	T/54	T/22
<i>Cirsium parryi</i>	T/100	T/40	.	T/33	T/9	T/11
<i>Clematis ligusticifolia</i>	1.0/100
<i>Cystopteris fragilis</i>	.	T/10	.	T/17	.	T/22
<i>Erigeron superbus</i>
<i>Fragaria bracteata</i>	.	.	T/11	.	T/9	.
<i>Fragaria ovalis</i>	.	T/20	T/67	T/33	T/27	T/11
<i>Geranium richardsonii</i>	.	T/10	T/67	T/33	T/9	T/55
<i>Dugaldia hoopesii</i>	T/100	T/60	1.0/89	T/33	T/18	.
<i>Heuchera parviflora</i>	T/100	T/10	.	.	.	T/22
<i>Hieracium fendleri</i>	T/100	T/30	.	T/33	.	.
<i>Lathyrus arizonicus</i>	T/100	1.0/70	T/55	.	T/27	T/11
<i>Lithospermum multiflorum</i>	T/100	T/20	T/67	T/83	T/27	T/22
<i>Oxalis alpina</i>	.	T/10
<i>Penstemon barbatus</i>	T/100	T/40	T/22	T/67	T/36	T/11
<i>Pseudocymopterus montanus</i>	T/100	T/60	T/55	T/50	T/27	T/11
<i>Pteridium aquilinum</i>	.	1.5/50	1.0/55	.	.	.
<i>Senecio bigelovii</i>	.	T/10
<i>Senecio neomexicanus</i>	.	T/10	T/22	T/50	T/9	.
<i>Smilacina stellata</i>	.	T/20	T/22	.	T/18	.
<i>Smilacina racemosa</i>	T/11
<i>Stellaria jamesiana</i>	.	.	T/11	.	.	T/11
<i>Swertia radiata</i>	T/18	.
<i>Thalictrum fendleri</i>	.	T/60	T/67	T/50	T/73	T/100
<i>Thermopsis pinetorum</i>	.	T/20	T/11	.	T/9	.
<i>Valeriana capitata</i>	.	T/20	.	3.5/33	T/18	1.0/100
<i>Vicia americana</i>	.	T/40	.	T/17	.	.

¹Occurrence of each species in each habitat type and phase is indicated by two values separated by a slash. The first indicates the mean density/plot for the tree species or the mean coverage/plot for the shrubs, grasses, and forbs. In all cases, however, the first value is the mean for only the plots in which the species was present. The value to the right of the slash is the percent constancy for each species in the habitat type and phase; it is the percentage of the total number of plots in the group in which the species was found. To indicate when a species had less than 1% cover, the letter T is used to the left of the slash. A dot indicates that the species was not found in a group. To show species occurrence, Moir and Ludwig (1979) use importance value, which is the product of mean density times constancy.



Alexander, Billy G., Jr., Frank Ronco, Jr., Alan S. White, and John A. Ludwig. 1984. Douglas-fir habitat types of northern Arizona. USDA Forest Service General Technical Report RM-108, 13 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Four Douglas-fir (*Pseudotsuga menziesii*) habitat types and two phases were identified from a reconnaissance survey of 46 Douglas-fir stands in northern Arizona. General descriptions of these habitat types are presented, and a key to their identification is provided.

Keywords: forest vegetation, plant associations, habitat types, forest ecology, *Pseudotsuga menziesii*, Arizona, Colorado Plateau.

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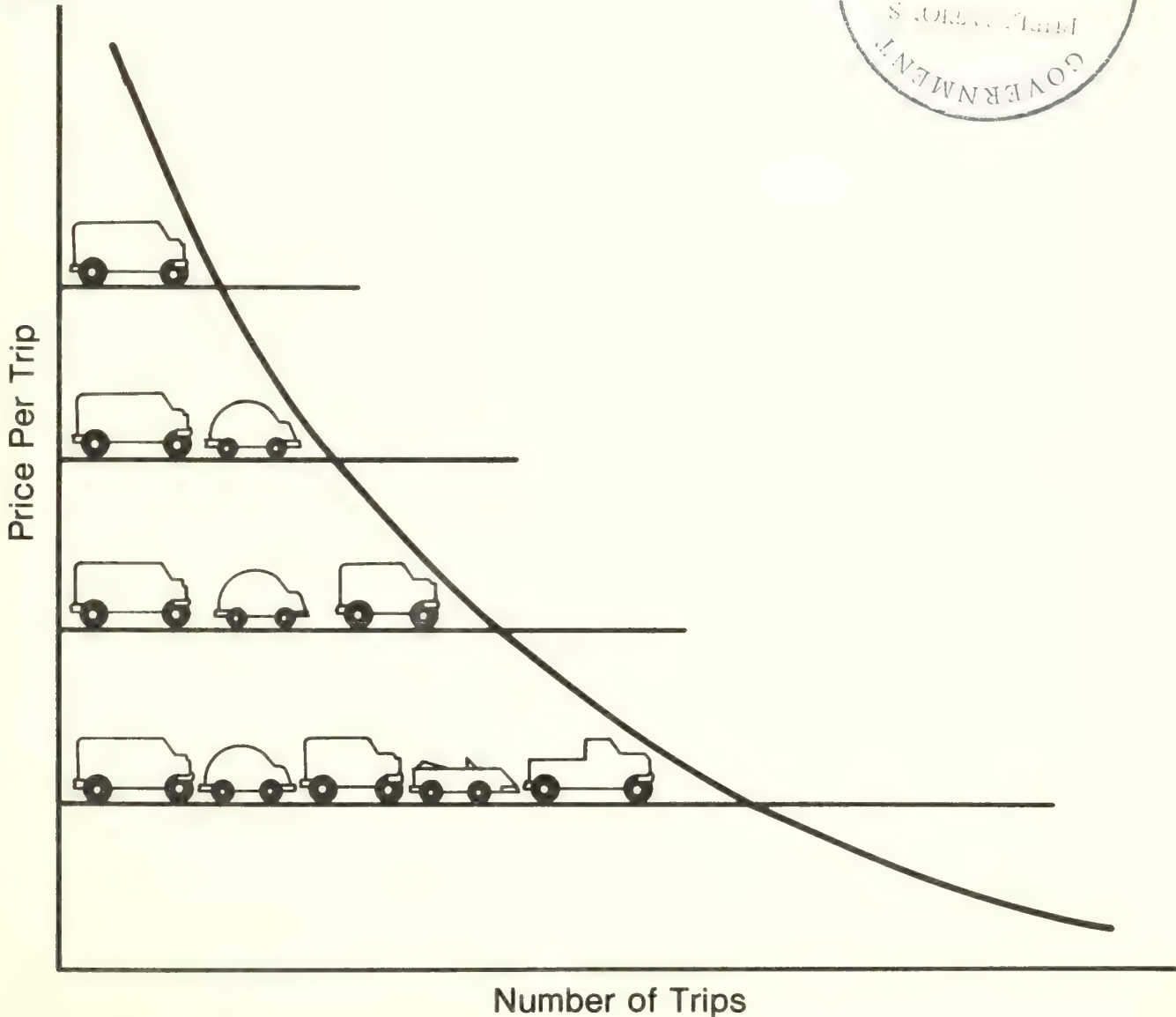
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Fort Collins,
Colorado 80526

General Technical
Report RM-109

The Travel Cost Model: Concepts and Applications

Donald H. Rosenthal
John B. Loomis
George L. Peterson



Abstract

The travel cost model (TCM) estimates the demand and supply curves for a recreation site in a manner commensurate with methods used for other resources. Therefore, dollar values estimated by the TCM are comparable to dollar values for other resources. Because of this, the TCM is well suited for use as an analytical technique in the study of recreation planning issues. Issues benefitting from TCM analysis include: the effect of raising entrance fees on visitation, the benefit of constructing a new recreation site, the benefit of modifying an existing site, and estimating use at existing or proposed sites.

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The Travel Cost Model: Concepts and Applications

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Contents

	Page
INTRODUCTION	1
HOW THE TRAVEL COST MODEL ESTIMATES THE SITE DEMAND AND SUPPLY CURVE	1
Assumptions of the Travel Cost Model	3
RELATIONSHIP OF TCM TO OTHER BENEFIT ESTIMATION TECHNIQUES	3
Monetary Valuation of Timber, Forage, and Water	3
Other Recreation Benefit Estimation Techniques	4
Contingent Value Method (CVM)	4
Administratively Assigned Values	4
Gross Expenditures	4
APPLICATION OF THE TRAVEL COST MODEL	5
Benefits from Construction of a New Site	5
Change in Benefits and Use for Modification of a Site	5
Value of Trip Versus Value of an Activity	6
Use of Travel Cost Models to Estimate Revenue and Quantity Changes for Price Increases	6
CONCLUSION	6
LITERATURE CITED	7
APPENDIX: CONCEPTUAL BASIS OF MONETARY VALUATION	8

The Travel Cost Model: Concepts and Applications

Donald H. Rosenthal
John B. Loomis
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INTRODUCTION

Management of public lands often requires that tradeoffs be made between marketed commodities, such as timber, and nonmarketed commodities, such as recreation. The Travel Cost Model (TCM) of estimating recreation demand can help with these tradeoff decisions. TCM provides information on the economic value of recreation opportunities that is commensurate with marketed outputs from forested lands.

The Resources Planning Act of 1974, as amended by the National Forest Management Act of 1976, requires that attention be given to economic efficiency (i.e., maximizing net economic benefits) in formulating forest plans. The TCM provides a way to bring public recreation services, usually a nonmarketed commodity, into this analysis. Specifically, information provided by the TCM can help to:

1. determine the net economic value of an existing recreation site;
2. determine the net economic value of creating a new site or modifying an existing site;
3. make more efficient allocation decisions among programs;
4. predict recreationists' travel behavior; and
5. forecast changes in the use of a recreation site resulting from charging fees (or changing fees) for using that site.

This paper explains what the TCM is and how it can be used to help manage recreation resources. The conceptual basis of the TCM is emphasized rather than details about how to actually build the model. The discussion of the TCM assumes the reader is familiar with basic microeconomic theory. Readers wishing a review of the relevant concepts from microeconomics should read the appendix to this report. That appendix gives a broad conceptual overview of the TCM within the framework of economic theory. The reasons why value estimates from the TCM are comparable to market prices for other commodities are explained in the appendix.

HOW THE TRAVEL COST MODEL ESTIMATES THE SITE DEMAND AND SUPPLY CURVE

The TCM estimates the demand curve for a recreation site by assuming that the price of consuming recreation at that site varies directly with the distance the consumer is from the site. The reason for the varying price is travel cost. At different prices (i.e., distances from

site), different quantities of recreation will be consumed; and these price quantity variations identify the site demand curve.

The rationale of Burt and Brewer (1971) is simplest and most direct. Consider a good that is produced exclusively at a fixed location. Let the consumers of the good be homogenous in all respects except location. Let them be dispersed geographically so that there is wide variation in the cost of reaching the site and returning, i.e., shipping the good to them. Also assume that the price to the consumer is the f.o.b. unit price (i.e., user fee), which is common to all, plus the unit shipping cost, which varies by location. The unit price at location i , p_i , is

$$p_i = p_o + t_i$$

where p_o = f.o.b. price
 t_i = unit shipping cost.

Thus, consumers at different locations face different prices because of the geographic variation in t_i . Transportation is simply a production input factor that varies by consumer location. This variable cost is passed on directly to the consumer.

Let the individual demand function for the recreation site for all consumers be the downward sloping line in figure 1. That curve shows the quantity of trips, q , a person will consume during a given time period at the price, p . The horizontal lines in figure 1 are the prices faced by consumers at various locations including the f.o.b. price, p_o , charged at the production site. Observation of p_i and q_i at various locations allows the demand curve to be estimated by appropriate statistical methods. Of course the demand function may not be linear, but alternative hypothesis may be tested and compared. In the case of the TCM, the demand curve in figure 1 represents the site demand curve, and each horizontal line shows the per trip cost of consuming recreation for recreationists living at different distances from the site. For example, the cost per trip of consuming recreation for person 2 is p_2 . The demand curve shows that at price p_2 , he will consume q_2 units (trips) of recreation from that site at a total cost of $0p_2dq_2$.

These horizontal per unit cost curves (actually supply curves) have nothing to do with the agency costs of providing the recreation site. They simply refer to the cost to the consumer, located at a particular distance from the site, of consuming recreation at the recreation site. A unique characteristic of the TCM is that the supply curve for a recreation site, as faced by the consumers,

varies from location to location. There are many supply curves, not just one. This variation in the supply curve allows estimation of the demand curve in figure 1. Because of the shifting supply curve between locations, points b, c, d, e, and f are observable and can be used in statistical analysis of demand.

The calculation of the net economic benefits to the consumer (i.e., total benefits minus costs incurred by consumers) of a recreation site simply entails adding up the area between the demand curve and the supply curves for the various users of the site. For example, recreationist 2 will consume q_2 units of recreation with total benefits equal to area $0adq_2$, the total costs are $0p_2dq_2$, and net benefit is p_2ad . Similarly, the net benefit to consumer i is p_1ac . The total net benefit of a recreation site to consumers is the net benefit to each and every consumer summed across all consumers. The net benefit of the site to society is the net benefit to consumers minus the costs of providing the site plus any receipts from fees. The unique characteristic of the TCM is that the demand curve is assumed to be reasonably common across consumers, but the price faced by consumers varies.

In the case of recreation, the consumer ships himself to the point of consumption, as with many private goods (e.g., shopping centers, movie theaters, etc.). This separates the shipment costs from the f.o.b. prices and creates some potential problems for the model. Because a consumer manages and directly pays the transportation cost, those costs may not be perceived correctly. Demand behavior for recreation will be sensitive to the perceived travel cost. These travel costs may be paid in a variety of ways including monetary expenditure, time, and effort. Identifying the travel costs a recreationist perceives he faces is one of the difficulties in applying the TCM.

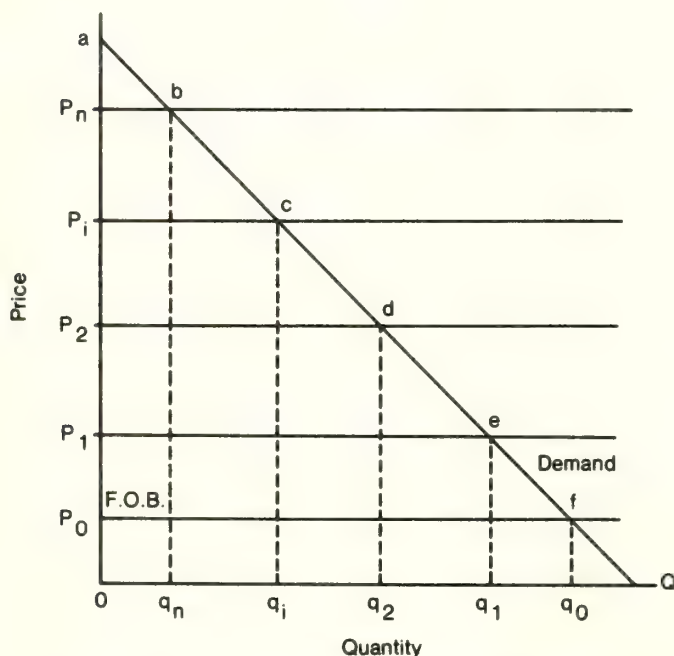


Figure 1.—Travel Cost Model Supply and Demand Curves.

Two additional aspects need explanation. First, there are two types of TCMs: the individual travel cost model and the aggregate model. What has been described above is the individual TCM.

The aggregate TCM is the same, except that people living near each other are grouped into an origin zone. All recreationists living in that zone, a county for example, are assumed to face the same per unit cost. The distribution of tastes and preferences is assumed constant across zones. In the zonal model, the quantity measure is the number of visits or visits per capita, from a given zone. The price for that zone is the average price per visit. Once the quantity measure is put on a zonal basis, the analysis is essentially the same as in the individual travel cost model.

The second point is that the demand equation estimated by the TCM is more general than simply relating price and quantity. Many user characteristics which potentially influence visitation, such as income or education, vary in addition to price. Furthermore, site characteristics will have a significant influence on demand. In its most general form the demand curve estimated by the zonal TCM is:

$$V_{ij} = f(C_{ij}, P_i, S_{ij}, A_j, D_i) \quad (1)$$

where V_{ij} = number of trips from origin i to site j

C_{ij} = cost of travelling from origin i to site j

P_i = population of origin i

S_{ij} = a measure(s) of substitutes to site j for origin i

A_j = a measure(s) of characteristics at site j

D_i = a measure(s) of characteristics of origin i , including income, and education.

This more complicated expression of the site demand curve does not change the underlying concepts related to benefit calculation, but it does complicate the mathematics. The site demand curve is now different for each origin zone.

In addition to being a benefit calculation tool, the site demand curve is an estimating model for recreation use. The general equation can be used to predict visitation at a new recreation site or estimate how visitation at an existing site will change if the characteristics of the site, the admission fee, the population surrounding the site, or access to substitute sites change. When predicted visitation is plotted against hypothetical admission fees, the resulting graph is known as the "second stage demand curve" (Dwyer, Kelley, and Bowes 1977).³ The use estimating ability of the general equation can be quite helpful when trying to decide how many people a facility should be designed to handle.

³The area under the second stage demand curve is also a measure of the net benefit to the consumer of the recreation site. The same estimate of net benefit will always result regardless of whether the procedures discussed in the text related to figure 1 or a second stage demand curve is used to calculate net benefit. This follows because the second stage demand curve is totally determined by the information in figure 1 or, more generally, from equation 1.

Assumptions of the Travel Cost Model

There are two categories of assumptions regarding the TCM. The first category addresses assumptions necessary to ensure that the use of travel costs as a proxy for price is correct. The second category addresses assumptions necessary to statistically estimate the demand curve. If these assumptions are grossly violated, the method is inappropriate and should not be used.

The key assumption necessary to interpret travel cost and travel time as a price of consuming recreation is that one can correctly measure key variable costs that affect trip making behavior. Here variable costs are the costs that vary with distance.

Quantifying variable costs to which trip-making behavior is sensitive is easiest when: (1) travel is incurred exclusively for visiting a site under study; (2) there are not benefits from the travel itself, so that the travel costs and travel time can be used to represent the price paid to visit the recreation site; and (3) the opportunity cost of travel time is known.

If a trip is for many purposes, travel costs are entangled in the joint production of several goods. It may not be possible to assign a portion of the trip costs to a specific purpose. For example, assume one takes a trip to visit friends as well as visit a recreation site. The total cost of the trip or a portion of the costs should not be arbitrarily assigned to the recreation site. The usual solution is to not use that observation as a basis for estimating the benefits of the recreation site. Suggestions have been made on ways to incorporate multiple destination trips into the travel cost model (Haspell and Johnson 1982).

It is commonly assumed that there is no utility or disutility to travel itself. If this is not true, travel cost and travel time do not represent the cost of visiting the recreation site. How to adjust travel cost estimates if this assumption does not hold is partly related to the issue of the opportunity cost of travel time.

Probably the most troublesome issue regarding the TCM is how to value travel time. The value assigned to travel time can markedly affect the benefit estimates derived from TCM. Many authors have discussed issues related to selecting a value for the opportunity cost of travel time (Cesario and Knetsch 1970, Cesario 1976, Wilman 1980, McConnell and Strand 1981). Empirical work reviewed by Cesario (1976) suggests that the opportunity cost of travel time may be between 1/4 and 1/2 of the wage rate. Whatever value is assigned to travel time, it must account for any utility or disutility to travel itself as well as the value of time in its best alternative use.

An analogy to timber production might help clarify the value of travel time issue. When logs are transported, time costs show up as labor costs. Similarly, when the consumer produces recreation trips, the time it takes to travel to the site is a production cost. Therefore, time costs are added to vehicle operating costs when calculating the "price" a recreationist must pay to visit the site.

The assumptions necessary to statistically estimate a travel cost demand function are the same as those required to estimate any other demand function.

1. There is sufficient variation in prices (travel cost) to statistically identify the demand function. This means that recreationists must come from enough different areas of origin to provide a range of distances by which to statistically trace out the demand curve. Violation of this assumption precludes statistical estimation, and, therefore the TCM cannot be applied.

2. All of the relevant variables that affect demand are properly represented in the TCM model (i.e., the functional form is correct). This is a standard assumption in statistical analysis that is necessary to get unbiased estimates of the slope of the demand curve. While the number of possible relevant variables is quite large, only a few make an important difference statistically. Besides travel costs, variables such as income, past experience with this type of recreation, availability of substitute sites, and attractiveness of the site in question, are among those found to be consistently significant or theoretically important. Further simplifying the task is that only variables that vary from person to person (or origin to origin in the aggregate model) need to be included. In the TCM, for example, the presence of bowling opportunities might influence visitation to a recreation site. However, if all zones are assumed to have equal bowling opportunities, this factor can be omitted from the TCM.

3. There is no shortage of the good in question resulting in unsatisfied demand. If, at a given price, there is more demand than supply, some of the demand will be unobserved. For recreation sites, this means that there must be enough capacity to satisfy demand. A technique for implementing TCM when there are capacity restrictions has been outlined by Loomis (1982).

RELATIONSHIP OF TCM TO OTHER BENEFIT ESTIMATION TECHNIQUES

Monetary Valuation of Timber, Forage, and Water

Brown (1982) describes a theoretical framework for valuing outputs of timber, forage and water yields from public forest lands. The methods presented for valuing those resources are conceptually equivalent to the TCM; however, a few comments regarding the valuation of these resources can be added.

In the case of a perfectly competitive stumpage market, the bid price for stumpage from a specific timber stand is a good measure of the net benefits to the producer of that stumpage. However, often the stumpage market is not competitive. The usual reason for lack of competition is that there is only one mill at which to sell the stumpage. With only one buyer of stumpage, the bid price is apt to understate the net benefits of stumpage. When there is not a competitive market, the value of stumpage is best estimated using the residual value timber appraisal system. That system estimates the net benefits of stumpage by determining the value of final products made from stumpage, which are sold in a competitive market, and deducting the costs of producing those products (i.e., harvesting, hauling, milling), and a margin for profit and risk.

It is commonly acknowledged that grazing fees are administratively set and do not necessarily reflect the value of forage. To determine forage values, the USDA Forest Service uses shadow prices from linear programs (Gee 1981). These shadow prices indicate how much returns can be increased over cash costs if an additional animal unit month is available. While the fee paid is in the \$1 to \$2 range, the value ranges from \$7 to \$16 per animal unit month. These shadow prices are commensurate with TCM values, because they both represent net benefit to the user per unit of output (i.e., the user's maximum net willingness to pay for the resource). For both forage and recreation, government costs are ignored when estimating values. Such costs become a consideration when determining appropriate funding levels for different programs.

To estimate the value of water, a variety of techniques are used (Young and Gray 1972). A commonly used technique is "change in net income," which is very similar to the residual value timber appraisal system used for timber. The change in net income approach applied to water calculates how much receipts and costs will change in a given area as the result of additional water supplies. The excess of receipts over costs is the economic measure of benefit. Again, these water values are commensurate with the values for other resources.

Other Recreation Benefit Estimation Techniques

Contingent Value Method (CVM)

The CVM or bidding games represent a different technique to estimate the net benefits to the user of a recreation site. In some cases TCM cannot be used, and CVM is a viable alternative to estimate the net benefit to the user of a recreation site. For example, there might not be sufficient variation in travel distances to an urban park to allow use of the TCM. To estimate net benefits to recreationists with the CVM, recreationists are asked to state the maximum additional fee they would pay before they would stop visiting the site altogether. The answer to such questions is a direct estimate of net benefits to the respondent because the figure given represents willingness to pay to visit a site above current expenditures. The CVM and TCM, therefore, are different methods of measuring the same thing.⁴ The CVM and TCM, as normally applied, do not "net out" the agency costs of providing the recreation site. These agency costs must be deducted to estimate the net benefit to society. If a fee is charged at the recreation site, the receipts should be counted as a benefit.

While some people object to the hypothetical nature of CVM and the invitation for untruthful responses, empirically derived CVM values often are below values based on other valuation techniques, such as the TCM or hedonic pricing (Bishop and Heberlein 1980, and Brookshire et al. 1982). The U.S. Water Resources Council (1979), which sets Benefit Cost Analysis rules for the Soil Conservation Service, U.S. Army Corps of Engineers, Bureau of Reclamation, and U.S. Fish and Wild-

life Service, indicates that TCM and CVM are the preferred valuation methodologies. Their use is required when recreation use levels or recreation benefits are above certain threshold levels. The TCM uses actual behavior to reveal a demand curve and estimate net benefits whereas CVM uses surveys of users to estimate net benefits. If CVM is used, the survey questions must be carefully worded and administered so as to avoid biased or meaningless answers.

Administratively Assigned Values

The other approach discussed by the U.S. Water Resources Council is Unit Day Value (UDV). Much like the USDA Forest Service's values for recreation, these values are administratively agreed upon measures of net willingness to pay for a particular type of recreation. In the case of the UDV, the analyst applies criteria related to quality, location, type of recreation opportunity, etc., to select a value. Administratively assigned values, while not conceptually different, are crude approximations, because there is little empirical support for using one set of values rather than another. If the same value is uniformly applied to all sites, it is much like saying an "automobile" is worth \$10,000 regardless of whether it is a Cadillac, Rolls Royce, Volkswagen, or Ford Pinto, and regardless of whether the user must travel 10 miles to buy it from a dealer or 2,000 miles to pick it up at the factory. In addition, the criteria used to vary the value from site to site have been criticized for lack of empirical support and subjectivity in applying them (Dwyer, Kelly, and Bowes 1977).

Gross Expenditures

This method uses the sum of all expenditures incurred by the recreationist as the value of the visit to site. There are several reasons why this is incorrect. Knetsch and Davis (1966) state, "Gross expenditures do not indicate the value of the losses sustained if the particular recreation opportunity were to disappear, nor do they show the net gain in value from an increase in a particular recreation opportunity." Gross expenditures only indicate the amount of money going into recreation support sectors of the economy resulting from availability of this site. If the site were closed, the same expenditure might be shifted to a different site or leisure activity. Thus, the flows of money might not be lost to the economy, just shifted from one area or sector to another.

Use of gross expenditures as a measure of value leads to maximizing inefficiency instead of efficiency. That is, if gross expenditures are a measure of value, new recreation sites should be located as far away from population centers as possible, so that people have to incur large expenditures to get there. This is unwise, because the travel costs saved by locating a site closer to major population centers could be spent to purchase other goods that also provide enjoyment. Use of the TCM allows for travel cost savings to show up as increased site benefits.

APPLICATION OF THE TRAVEL COST MODEL

Benefits from Construction of a New Site

Assume that the construction of a new campground is being considered, and one criterion to be considered in the decision is benefit-cost analysis. In this context, the benefits of constructing the campground include the value of the camping experiences that will be provided at the campground, as well as the value of enhancements to experiences provided at other campgrounds where reductions in congestion may have resulted from use being shifted to the new campground. Costs include what must be foregone in order to provide the camping experiences, including construction and operating expenses for the campground, and outputs that must be foregone for the area influenced by the campground such as possible reductions in the output of timber and noncampground based recreation. Other changes in the value of forest outputs that are expected to result from the construction and operation of a campground also should be evaluated.

For the purposes of this report the discussion is limited to assessing the benefits of the construction of the new site that accrue at the new site. Readers interested in the condition under which one does and does not take into account the effects on existing facilities of introducing a new facility should consult Cesario (1980) or Knetsch (1977).

The basic travel cost model is an equation that predicts visits from particular origins to the site. As such, it includes those variables that are expected to influence site use including distance to site, site characteristics, and the availability and characteristics of substitute sites. In evaluating the benefits of a proposed new site, the first decision is whether or not to employ an existing model. If an existing model is employed it is important that the model (i.e., the equation that predicts visits from particular origins to the site), be applied to the proposed campground, and not the values per visit or day derived from its application to another site. The values derived from application of a travel cost model to a particular site depend on the characteristics of that site, the alternatives that are available, the population of the market area, and the location of the market population with respect to the site and alternative sites. Because all of these factors vary from site to site, the dollar value derived from application of the model at one site is not appropriate at another site, unless the two sites are very similar in all of these respects.

Estimating the model involves considerably more work and expertise than using an existing model. If a suitable model has already been developed, then it may be used to estimate use and value. When estimating a TCM model a variety of statistical and theoretical issues need to be addressed. While these issues are not overly complex, using an existing model simplifies matters.

In selecting a TCM equation to estimate the willingness of users to pay for the use of a proposed site, it is preferable to choose a model estimated for a similar site or set of sites in the same region as the proposed site. That model should reflect the influence of alternative

sites and the characteristics of the campground and surrounding areas on the willingness of users to pay for the use of the site. If the model does not include the site characteristics, then it is essential that it was estimated for a site with similar characteristics to the one being evaluated. If the model was estimated for a site that did not have substitutes, extreme care must be taken in applying it to a site that has substitutes. For an illustration of adjustments in the model that might be made in this case see Knetsch (1977). If adjustments are not made, the value of the proposed site will be misestimated; omitting substitutes from the model can result in either over- or under-estimating the value of the site.

If, after reviewing the literature and checking agency records for available models, a suitable model is not found then a new one must be estimated. The reader is referred to Dwyer et al. (1977) for details on estimating a new model.

The TCM estimates the value to users of the new site, given the existence of other sites. Specifically, the total consumer surplus estimate from the TCM model is an estimate of the willingness of users to pay for the site over and above the travel costs they incurred in getting to the site and any entrance fees charged. The TCM estimates are the total benefits minus costs which are incurred by users of the recreation site. The greater the number of substitute sites and the closer those sites are to the one being proposed, the lower the proposed site's value is likely to be. The TCM model, therefore, estimates the value of a recreation site at the margin.

The construction of a new campground may reduce the use of nearby campgrounds. If these other campgrounds are heavily used and congestion is reduced by the creation of the new site, the increase in the willingness of users of those campgrounds to pay resulting from that reduction in congestion should be considered as a benefit of the newly constructed campground. These changes in benefits at other sites ordinarily would not be estimated by direct application of travel cost models. Conversely, the creation of a new recreation site may increase congestion at adjacent sites. This increase in congestion at neighboring sites should be considered a cost in terms of the newly proposed project. However, if the new site affects only the quantity of use at other sites, and not quality, the change in benefits at other sites should be ignored (Cesario 1980).

Losses in the value of timber and other outputs expected to result from construction of the new site also should be considered as costs. The cost may take the form of decreases in the value of timber sold because of higher harvesting costs incurred as a result of efforts to protect the campground and surrounding areas. The values assigned to these losses, which should be in the form of stumpage prices, can be estimated from timber sales in the area or using timber sale appraisal procedures.

Change in Benefits and Use for Modification of a Site

To estimate the change in benefits associated with the modification of a site, it is necessary to estimate the benefits with and without the modification. This can be done

by developing a single TCM equation estimated over a wide range of site conditions and including variables that reflect the proposed modification. The model would be solved with and without the modification and the results compared. Alternatively, two travel cost models could be used, with one predicting the value without the modification and the other predicting the value with the modification. The difference between these two values would be attributed to the modification.

Value of Trip Versus Value of an Activity

A person who visits a recreation area normally participates in many different activities. For example, a visitor to a USDA Forest Service campground might hike, fish, swim, picnic, as well as camp. The TCM gives an estimate of the value of the entire trip, not specific activities. The normal application of the TCM gives no information about which specific activity created the value. Value probably was contributed by all the activities.

In recording recreation use, government agencies often estimate the number of visitor-hours or recreation-visitor-days (RVDs) of different types of activities. Inconsistent bookkeeping creates a problem. Using TCM trip values to estimate the value of an RVD for a particular activity when several activities were engaged in is incorrect. Because trips often involve multiple activities, apportioning the entire trip value to various activities is very difficult, if not impossible, to do without additional information. If all the value is assigned to one activity (e.g., major trip purpose), the value of that activity will be overstated. The simplest solution is to report values as the value of a trip to a certain site.

As a tangent, the simple TCM also gives no information on what proportion of the value of a trip was produced by nature versus what was produced by management. Again, the way to get this information is to include management characteristics in the demand equation. Unless this is done, TCM says little about the efficiency of investing money to change the management characteristics of a site. Of course, if the recreational use of an area is to be eliminated (or created), this information is not needed as the total value will be lost (or gained).

Use of Travel Cost Models to Estimate Revenue and Quantity Changes for Price Increases

Travel cost-based demand curves have been estimated primarily for predicting the willingness of users to pay for the use of a site. For that purpose, it is necessary for the area under the estimated site demand curve to closely approximate the area under the true site demand curve. With increasing interest in pricing as a management tool, attention has turned toward the use of demand curves to predict changes in use and revenue with various levels of entry fees. For this purpose, it is important that the estimated demand curve closely approximate the true demand curve in the lower right section (i.e., at low entry fees).

Limited experience suggests that some of the travel cost-based demand curves estimated with prime attention to the area under the curve may not be highly useful for predicting responses to small increases in the price charged for the use of recreation sites. It seems that these curves estimate very large reductions in site use with small increases in fees—something that does not usually happen.

One possible explanation for this discrepancy is that the single site TCM predicts quantity decreases if the prices at the site in question are raised and all other prices remain constant. In reality, an agency usually raises prices for an entire system of recreation sites. This affects the price of substitute sites, and, as a result, the decrease in use at any particular site will be less than predicted by a single-site TCM. More experience with the TCM, especially regional TCMs, in conjunction with pricing is needed to assess the ability of TCM to accurately predict quantity decreases from price increases.

CONCLUSION

The TCM gives estimates of the net economic benefit to the user of a recreation site. More specifically, the TCM estimates the willingness of users to pay for the right to use the recreation site over and above their existing costs. Agency costs of providing a recreation site are not deducted from the net benefit estimates. The techniques used to develop value estimates for recreation are entirely commensurate with techniques used for other resources (Brown 1982).

There is no problem in comparing market price to average consumer surplus. In all cases, the area between the demand and supply curves for the project or good in question is a measure of net benefit. If the net benefits of a project are divided by the quantity of output produced by that project, the resulting number is the net benefit per unit of output. As discussed in the appendix, net benefits are calculated in a similar manner for all outputs.

The TCM identifies the demand curve for recreation sites by utilizing price-quantity variations from different persons (or origins in the zonal travel cost model). The value estimate of the TCM indicates the value of a recreation site to users, given that all other sites exist as substitutes to that site.

The TCM may be used in a variety of circumstances. Most important, it can be used to help make resource allocation decisions concerning what is the best use of a given parcel of land. In employing the TCM, it is not always necessary to estimate a new model for each given recreation site. In many instances it is possible to employ the TCM demand equation estimated at another recreation site to determine the value of a different site. It is important that the model be used at the new site, as opposed to the values generated from the use of that model at another site.

The TCM is far from being precise in all its value estimates. More work needs to be done in the areas of

functional form, value of travel time, multiple destination trips, modeling substitutes, and the regional TCM. However, the state-of-the-art has advanced to the point where useful estimates for the value of outdoor recreation can be obtained.

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APPENDIX

CONCEPTUAL BASIS OF MONETARY VALUATION

In the framework of economic efficiency, resources should be allocated so as to maximize net economic benefits. Net economic benefits are total economic benefits minus total economic costs. Economic benefits and costs are often different than financial economic benefits and costs. The latter are restricted to actual dollars exchanged. Economic benefits and costs include financial considerations but also take into account benefits and costs which are not represented in the marketplace. For example, an economic cost of burning wood to heat a home is air pollution in the surrounding community. This is not a direct financial cost to the homeowner but it is an economic cost to society.

Microeconomic theory indicates that the area under the demand curve for a commodity represents the total benefits of consuming that commodity. If all consumers of the commodity paid their maximum willingness-to-pay (e.g., if units of the commodity were sold by sealed bid and given to the highest bidder), then the area under the demand curve represents the maximum obtainable revenue from such a sale. Similarly, the area under the supply curve represents the total cost of producing the commodity. Therefore the area between the demand and supply curve represents net economic benefit.⁴

These concepts are illustrated in figure 2, which depicts the situation where d units of a good are sold at price P_1 . The total willingness to pay for those d units of a good is the area bounded by $Obcd$. The total cost of providing d units of the good is area $Oacd$. The net benefit is the shaded area abc . The net economic bene-

⁴For this to be true it must be assumed that all relevant benefits and costs are represented by the curves. For example, when calculating the net benefit of burning wood it must be assumed that pollution is not an important issue or has already been incorporated into the demand and supply curve.

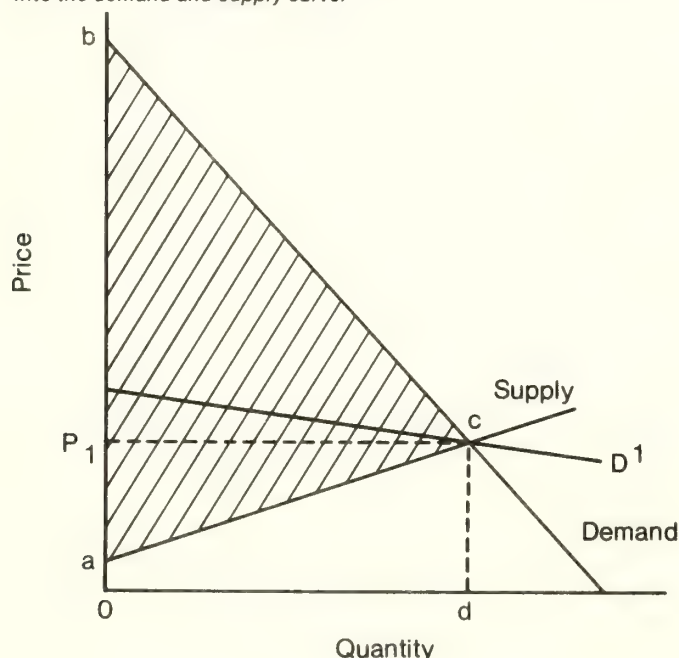


Figure 2.—Demand and Supply Curves.

fits are often broken into two parts—consumer surplus, area P_1bc , and producer surplus, area aP_1c . Figure 2 shows that net economic benefit is simply the sum of consumer surplus plus producer surplus. Producer surplus is actual revenue received by the producer over and above costs. Consumer surplus is the difference between the maximum which consumers would have been willing to pay for the good, and their actual expenditures. Producer surplus exists because some firms can produce products more cheaply than others. With a fixed price, efficient firms receive a surplus. Similarly, consumers who highly value a good are apt to enjoy consumer surplus because they pay the same price as everyone else.

When d units of the good are produced and sold at price P_1 the net economic benefit of producing one more unit of the good is zero. This is because the cost of producing one more unit of the good exactly equals the willingness to pay for one more unit of the good. In figure 1, both the cost and willingness to pay for an additional unit of the good are the price at which it is being traded in the market, P_1 .

If the demand curve in figure 2 were actually D^1 , then there would be little consumer surplus, but price would be unchanged. The steepness of the demand curve above the market clearing price determines the amount of consumer surplus. If the demand curve were a horizontal line at P_1 , then there would be no consumer surplus.

Slopes of Demand Curves

There are important differences between the demand curve faced by the industry and the demand curve faced by an individual firm within the industry. The left graph in figure 3 shows the industry-wide demand and supply curves which indicate the amount of the commodity that would be demanded by all consumers and produced by all firms, respectively, at particular market prices. The equilibrium price is P_e , when Q_e units of the commodity are sold.

If the industry in question is competitive, then an individual firm within the industry will produce a very small portion of the industry-wide output. For example, in figure 3, one firm might produce $Q_e q'_s$ units of output. If that firm enters (or leaves) the industry the equilibrium price will fall (or rise) slightly so that the new quantity clears the market. If q'_s is infinitely close to Q_e , as is the case in a perfectly competitive market, then the presence or absence of the firm will not affect the equilibrium price. The total benefits of a firm whose output is $Q_e q'_s$ entering the industry is represented by the shaded column in the figure. That area is approximately the market price times the quantity of output (i.e., $P_e (Q_e q'_s)$). The closer q'_s is to Q_e , the more exact the price times quantity measure will be.

If the market is perfectly competitive, then the demand curve faced by an individual firm is a horizontal

ne at price P_e , as shown in the right graph in figure 3 (Gould and Ferguson 1980). The major reason for this is that the output from that firm is so small, compared to industry output, that the actions of the firm do not affect the equilibrium price. An individual firm may sell as much or little as it pleases at the going market price. If a firm tries to sell at a price greater than P_e , no one will buy from that firm because there are other firms willing to sell the product at price P_e . This, of course, assumes all firms provide identical products.

When a demand curve is horizontal, the area under it, and hence total benefit, is calculated by multiplying price times quantity (i.e., $P_e \cdot q_s$ in figure 3). If this same area were calculated on the left graph of figure 3, it would be a very skinny column, similar to the one shown. The shape changes because of the different horizontal scales in the two graphs.

The net benefit of production from a single firm is, as usual, the area between the supply and demand curve for that firm (i.e., area aP_eb in the right graph of figure 3). The important points to note are that: (1) there is no consumer surplus associated with the production of a single firm in a competitive industry, and (2) under these conditions price times quantity gives an accurate measure of total benefits.

Under certain conditions, the demand curve for marketed commodity from an individual firm might be downward sloping. First, if the delivery of that product from its point of production to its point of use involves substantial transportation costs, the demand curve is apt to be downward sloping. For example, the demand curve for sand and gravel from a particular site is downward sloping because of significant transportation costs. A sand and gravel firm cannot sell all the materials it desires at a fixed price because transportation costs greatly limit the amount that distant customers are willing to pay for material at the site. In evaluating the total benefits of operating or creating a sand and gravel operation, a price times quantity measure would not be correct. In that case, the downward sloping demand curve for sand and gravel from that specific site would have to be estimated.

A second case in which the firm demand curve is downward sloping occurs when the output from a specific firm is a substantial portion of the industry-wide

output. For example, if stumpage production from a specific timber stand increases output by such an amount that the price of stumpage in an area is lowered, then the demand curve for stumpage from that stand is downward sloping. The greater the price changes, the greater the slope. Demand for stumpage is currently modeled by regions within the country (Adams and Haynes 1980). With this type of model, it is reasonable to assume that production from individual stands on a National Forest does not affect the regional price.

Market Price Versus Consumer Surplus

The question is often raised as to why consumer surplus is used to value recreation opportunities and market prices are used for other commodities such as stumpage. The answer is that net economic benefit is actually being used in both cases. The market structures and pricing policies are different for recreation and stumpage. Therefore, the slopes of demands curves for recreation from a specific site versus stumpage from a specific site are different.

The stumpage market often, though not always, is assumed to be competitive; so, there is no consumer surplus associated with production from a single site. As a result, net benefit can be calculated as previously described using market price and the supply curve. In contrast, the recreation opportunities from a specific site are not exchanged in a competitive market; therefore, the demand curve and supply curves for a specific site must be estimated to calculate net benefits.

A recreation site has a downward sloping demand curve because travel costs and site characteristics create a distinct market for each recreation site. That is, an opportunity to recreate in Maine is probably not a good substitute for the opportunity to recreate in New York. Creating a recreation site is likely to make large changes in the price of consuming recreation for individuals living around that site. For individuals living reasonably close to the new site, the price of recreating (including vehicle operating costs, time costs, and entrance fees) would be substantially reduced. This reduction in price generates significant consumer surplus for the recreationist.

The shape of a demand curve for recreation from a specific site is better represented by the left graph of figure 3, and the shape of a demand curve for stumpage from a specific site is represented by the right graph. However, the graphs represent extreme cases and two important points must be considered: (1) the true demand curves for stumpage and recreation are not exactly as represented by these extreme cases; and (2) the situation varies from site to site. Nevertheless, this rather extreme contrast between stumpage and recreation curves will be maintained here for illustrative purposes.

In the case of stumpage, the reason the demand curve is horizontal is that in a competitive market there are perfect substitutes for stumpage from that site. The substitute is stumpage from other sites. If there are many bidders for the stumpage in question and many mills

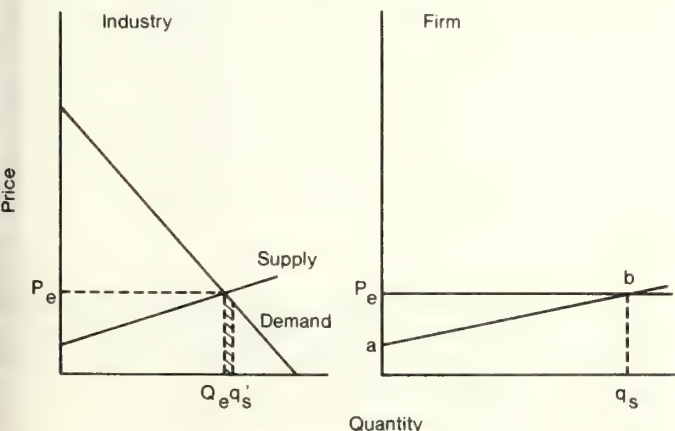


Figure 3.—Industry Versus Firm Demand.

able to sell the stumpage, the market is probably reasonably competitive. In a competitive market, price at the mill (in this case, price is the bid stumpage price per thousand board feet (MBF) plus harvesting and hauling costs per MBF) times quantity (MBF) is a good measure of the total or gross benefits of stumpage from that site. As usual, net benefit is obtained by subtracting total cost from total benefit. Transporting of sawlogs from the harvesting site to the mill entails substantial costs. Because some sites are closer to the mill than others, they will command higher stumpage prices. These higher prices can be counted as a benefit, just as consumer surplus is in the recreation case.

In summary, if the demand curve for stumpage from a site is horizontal, total benefits can be estimated by a price times quantity measure. The slope of the demand curve depends on the market structure. In contrast, because of its downward slope, the demand curve for recreation from a site must be statistically estimated and the area under it calculated to estimate total benefits.

Average Consumer Surplus in a Recreation Model

The net benefits of the goods and services provided by a public project can be expressed as:

$$NB = TB - C_{ag} - C_{pr} + F$$

where NB = net benefits
 TB = total benefit
 C_{ag} = agency or government costs
 C_{pr} = all other private (non-agency) costs, including fees, (e.g., recreationists' travel costs)
 F = fees collected for right to use or have the public resource.

As previously stated, the project is worth undertaking if the net benefits are greater than zero. From an economic efficiency viewpoint, a project is worth undertaking if:

$$TB - C_{pr} + F \text{ is greater than } C_{ag}.$$

For purposes of this paper, total benefit is equivalent to the maximum willingness-to-pay for the right to use or have a good or service.

Consider the case of a project which produces two million board feet of stumpage from a given parcel of land. Assume that the f.o.b. (free-on-board) price of lumber from the stumpage at the mill in a competitive market is \$100 per MBF, and that the cost of harvesting stumpage from the site, milling the logs, drying and selling the lumber, and allowing a normal rate of profit, is \$90 per MBF. Based on these assumptions, the total benefits of stumpage from that site are \$200,000, and the costs to the operator to receive this \$200,000 are

\$180,000. The net benefits of this project, excluding Forest Service costs, are \$20,000,⁵ or \$10 per MBF. Assuming the road system is already in place, so as to not confuse the discussion with road credits, \$10 per MBF will be the competitively bid stumpage price. A \$10 per MBF the operator earns a normal rate of return on his investment. This \$10 per MBF is producer surplus which accrues to landowners, in this case the government. Alternatively, it may be thought of as rent on the land. It is a payment to the landowner for the right to harvest the stumpage. If the project costs less than \$10 per MBF to prepare and administer, it ought to be undertaken, assuming there is no alternative use of the land which would yield greater net benefits.

In the case of recreation, the TCM might indicate that the total benefits are \$80,000 and that the costs of producing this \$80,000 worth of benefits is \$70,000. The costs in the framework of the TCM are entirely travel costs borne by the recreationists. Travel costs are analogous to harvesting, milling, drying, and selling and costs plus a normal rate of profit in the previous example. The net benefit of this recreation site, exclusive of Forest Service costs, is \$10,000. This \$10,000 figure is what is normally reported in the results of travel cost studies. In other words, the travel costs incurred by recreationists are netted out of the total benefit estimates before the estimates of a recreation site are reported. If this site in question had 3,000 recreation visitor days (RVDs) per year, then the net benefit to the consumer per RVD would be \$3.33.

If fees are collected at the recreation site, then receipts can be counted as a benefit. If \$5,000 of the \$70,000 worth of costs mentioned above were recreation fees, the net benefit of the site would be \$15,000. The fee receipts are not consumer surplus, but they can legitimately be counted as a benefit. Similarly, receipts from timber sales are benefit.

The \$10 per MBF net benefit for stumpage and the \$3.33 per RVD net benefit for recreation are entirely analogous figures. Both are expressions of the net benefit per unit of output produced, without a deduction for C_{ag} . The recreation benefits per RVD are referred to as average consumer surplus, because the source of the net benefit is consumer surplus. Similarly, the source of value for the stumpage is producer's surplus, and these figures could justifiably be called average producer's surplus. However, the simplest way to look at it is that in both cases the figure represents the net benefit per unit of commodity produced, without a deduction for C_{ag} from a given parcel of land. The rationale for comparing competitively bid stumpage prices to average consumer surplus per RVD is now complete. Of course the argument could be extended to other marketed goods from wildlands, e.g. minerals.

⁵When calculating net benefit the opportunity cost of using the land for a given purpose should be deducted. In this case, if the land could return \$5,000 in the next best alternative use, then the net benefit from stumpage production is \$15,000.

Rosenthal, Donald H., John B. Loomis, and George L. Peterson. 1984. The travel cost model: Concepts and applications. USDA Forest Service General Technical Report RM-109, 10 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

The travel cost model (TCM) estimates the demand and supply curves for a recreation site in a manner commensurate with methods used for other resources. Therefore, dollar values estimated by the TCM are comparable to dollar values for other resources. Because of this, the TCM is well suited for use as an analytical technique in the study of recreation planning issues. Issues benefitting from TCM analysis include: the effect of raising entrance fees on visitation, the benefit of constructing a new recreation site, the benefit of modifying an existing site, and estimating use at existing or proposed sites.

Keywords: Travel cost model, willingness to pay, economic efficiency, valuation

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

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Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

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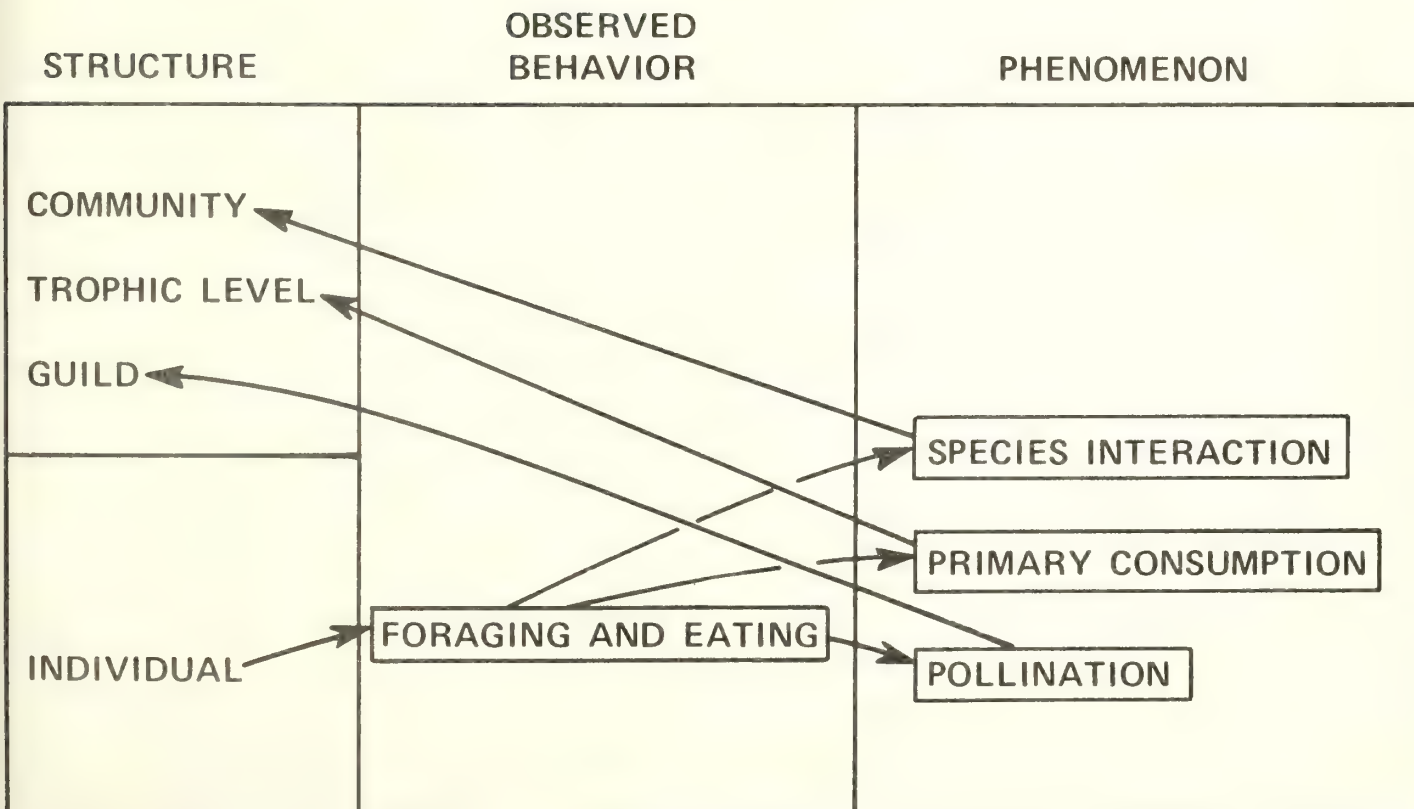
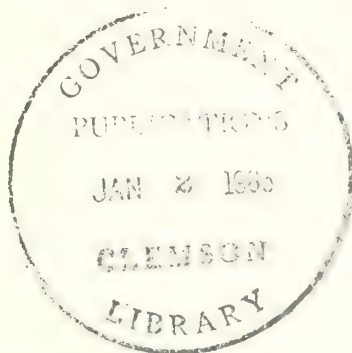
Fort Collins,
Colorado 80526

General Technical
Report RM-110



Interlevel Relations in Ecological Research and Management: Some Working Principles from Hierarchy Theory

T. F. H. Allen, R. V. O'Neill, and T. W. Hoekstra



Interlevel Relations in Ecological Research and Management: Some Working Principles from Hierarchy Theory¹

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Abstract

This report clarifies the role of the observer and what he observes as an aid to ecological research and natural resource management. It describes what is involved in observing complex natural systems, the role of the observer in moving through surfaces of natural systems, and finally summarizes, from these, the important principles in linking levels of natural systems that emerge.

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T. F. H. Allen, R. V. O'Neill, and T. W. Hoekstra

Introduction

Ecologists study complex systems which span many levels of organization (e.g., organisms, populations, and communities). As a result, ecologists face the difficult problem of linking levels of organization. Differences in criteria for organization and dynamic behavior make simple aggregation of lower levels insufficient to explain higher levels. What is needed is a set of working principles that allow the ecologist to keep track of terms and data between levels.

Although criteria for organization change between levels, there are consistent patterns that order interlevel relationships and perception of those relationships. For example observations made with coarser grain resolution will necessarily detect high levels of organization as long as observational criteria are held constant. Furthermore, this is true independent of which criteria are actually used for observation be they physiological, floristic, or hydrological. Also, sets of observation extending over larger areas and/or longer time will similarly be able to detect higher levels of organization. Thus, grain and extent are crucial to ordering perception of levels. Perception of higher or lower levels involves the passage of the ecological observer through what are functionally ecological surfaces. Surfaces are crucial to defining levels.

Ecologists often are faced with coupling the level that contains readily perceived objects (i.e., organisms) to other levels where there are valid but less tangible entities (e.g., ecosystems). Moving to lower levels sometimes demands observation of entities (e.g., microbes) and processes (e.g., stomatal opening) much smaller than ordinary human perception. Moving to higher levels of organization, the entities are also hard to perceive and several observations must be conceptually linked before the structure emerges.

Higher levels of organization are particularly troublesome. Ecologists have only recently possessed computational power commensurate with physically large systems. Inexperience with complex systems is sometimes brought home with unkind force, when dust bowls arrive in real time or when computer simulations produce absurdities. Nevertheless, society recognizes pressing problems precisely in these large scale systems, and it demands, quite fairly, that ecologists contribute to solutions. For example, the 1974 Forest and Rangeland Renewable Resources Planning Act requires that each decade the USDA Forest Service not only report on the status and trend of forest, wildlife, range, recreation, and

fisheries resources at a national level, but also that it translate effects of local management practices into national level programs to support national needs. It seems to be ecology's responsibility to link small scale systems production estimates to production in large scale complex systems, but how to start?

Prior to the American effort in the International Biological Program, it was believed that ecological systems could be almost perfectly simulated, given enough electronic memory and sufficiently fine-grained data. Few would maintain that today. Apparently, there is more to complex systems than lots of little bits of information. Part of that "something more" may be found in the hierarchical organization that structures complex systems (Allen and Starr 1982).

This report examines general ways to study complex systems, and develops general principles pertinent to such problems. These principles are derived from a detailed analysis of what an observer of a complex system will experience, and the precautions that must be taken in linking levels of organization. While the principles have much generality, the focus is on complexity in systems of particular concern to ecologists.

Observing Complexity

Role of Surfaces

Two distinctions are needed to characterize a hierarchical system. First, there is the distinction between structural entities at a given level of organization (e.g., the distinction between two trees). Second, there is the distinction between successive levels (e.g., between trees and the forest). The two distinctions are related. On the level at which trees are distinguished, the interesting behavior involves how one tree interacts with another. At the "forest" level distinctions between trees are lost, but boundaries, such as forest edges, are recognized.

Hierarchies are, in the most general terms, partially ordered sets (Sugihara 1983) where there is an asymmetry of relationship between elements. Several criteria are particularly helpful for defining asymmetry in ecological hierarchies. These criteria define higher levels as (1) containing (in nested system.s), (2) constraining, (3) the context of, (4) behaving at a lower frequency than, and (5) exhibiting less bond strength than, lower levels (Webster 1979).

The definition of any structure may be seen in terms of these criteria. A complex structure is made of smaller structures and is a component of a higher level of the hierarchy (fig. 1). The entity to be defined is contained by its outer surface (criteria 1-3). Surfaces in space are those places around which the strength of interaction is most variable. Inside a surface there is a collection of parts with strong interactions (criterion 5) and rapid exchange (criterion 4) (Simon 1962, 1973). Thus, surfaces define separate entities and are responsible for the characterization of discrete levels of organization (Allen and Starr 1982).

Now introduce an observer to see what effects surfaces have upon what is observed. Consider exchange across a surface that is weak and sluggish (Platt 1969). An observer inside the surface detects high frequency behavior associated with rapid exchanges among components (fig. 2). An observer outside sees slower behavior characteristic of interactions among higher level entities (fig. 3). Thus, the surface is defined by a change of frequency, sandwiched between high frequency behavior inside and low frequency exchanges outside. The relationship of the surface to the observer is crucial to determining what is observed.

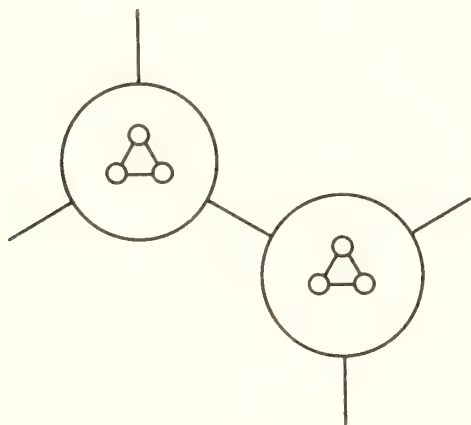


Figure 1.—A hypothetical system with various parts visible under different protocols for observation. The full system is composed of two entities, each with three parts. The complete system is not visible within any single observation set.

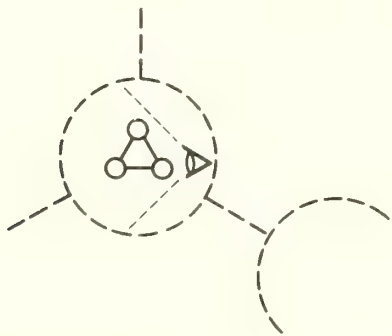


Figure 2.—Inside the surface, looking inward, is the only position from which the parts and their interconnections can be seen without distortion. (The eye indicates the position from which the system is observed.)

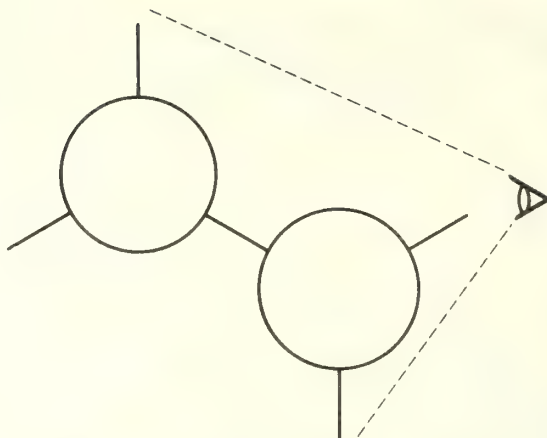


Figure 3.—If the observer moves far enough away from the surface, the other whole is identifiable as a separate entity, responsible for part of the environmental influence. (The eye indicates the position from which the system is observed.)

Relax the requirement that surfaces be situated in certain places in space, and the essential features remain; configurations that define observable entities can still be detected. For example, the Krebs Cycle can be distinguished as an entity, even though its enzymes, substrates and products all interdigitate with a mixture of other organic molecules. Similarly, cycling pathways may be detected in ecological nutrient data. The pathway is adequately defined by frequency characteristics even though the cycle cannot be mapped on the ground. It is the difference in reaction rates within, as opposed to without, that defines the entity (Levins 1973).

A critical characteristic of surfaces is their power of integration (Platt 1969; Simon 1962, 1973). Thus, for example, the surface of a community may be recognized by the way component biota are integrated into an interacting unit. The fact that this surface does not map easily onto a particular part of three-dimensional experiential space is, for present purposes, superfluous. This approach to surfaces provides a tool for dealing with levels where there are intangibles above and below the level of commonplace human experience. Discussion of surfaces, henceforth, will include these intangible surfaces as a normal case.

Observation Sets

Because of the importance of surfaces in distinguishing entities and levels of organization, researchers and managers must be explicit about how they look at an ecological system and detect the surfaces. The critical concept here is the observation set. An observation set defines how the investigator decides to look at a system. Two decisions are required. First, the investigator chooses the objects of study. He picks the level on which he will focus; this, in turn, determines the structural entities he will discriminate (Rosen 1977). In other words, the investigator must decide if he will look at cells, organisms, guilds, or communities. Second, the investigator must decide on the phenomena of interest. He chooses those changes in the objects of study which will

be considered as interesting (Pattee 1978). Thus, although he has decided to look at populations as his object of study, he must still decide whether he is interested in, say, the phenomenon of growth (i.e., changes in numbers through time) or migration (i.e., changes in numbers over space).

The observation set begins with a data set, but goes beyond just a collection of raw measurements. The observation set is the means to observe in a scientific manner. It is coupled to a procedure for collecting data, such as tree densities in 0.1-ha plots or fluorometric readings of plankton chlorophyll. More than this, scientific observation involves methods of analysis such as Fourier transformation or ordination of binary transformed data. Observation also involves criteria for identifying significance (statistical or otherwise) in the results of analysis. Only when the raw data are analyzed and the significance of the analysis is recognized, is the critical role of observation complete. The observation set depends upon the scientist's paradigm (Kuhn 1962) and is deeply influenced by the way he considers his object of study.

A pH meter reading alone does not constitute an observation set because observation is not complete without fixing (1) the procedure for taking the readings, (2) the interval between the readings, (3) the degree to which the readings are to be integrated, e.g., by averaging over time and space, (4) the extent in time and space of the entire universe of observation, and (5) the criteria for significant change in the readings. In an observation set the concern is not just with system configurations frozen in a set of encounters with the meter, but also with the dynamics inferred from differentials between individual measurements.

Grain and Extent

Observation sets distinguish entities and levels by virtue of the surfaces detected. Two particularly relevant aspects of observation sets at this point are grain and extent, both of which position the observation set with respect to surfaces.

Grain determines the fineness of the distinctions that can be made in an observation set. Sampling more often or employing an analytical procedure that preserves fine distinctions, both make the observation set more fine grained. Lower level entities can only be seen in a fine-grained observation set which preserves the fine distinctions needed to discriminate between small things. Thus, in a time series, sampling intervals must be kept short to detect high frequency behavior. Grain determines the lower limits of observation and fixes the finest possible level of resolution in an observation set.

In contrast, extent determines the largest distinctions (i.e., the largest surfaces) that can be seen. If the characteristic behavior of a relevant large entity takes longer to occur than the period of the entire sampling regime, then the behavior can not be seen. Sampling for one summer season does not allow a plankton ecologist to address phenomena associated with the annual cycle. The difference between successive summers can only be

studied if the observation set is extended to cover two or more summers. Sampling for only one summer fixes the extent so as to deny access to annual phenomena no matter what the mode of analysis.

The detection limits imposed by grain upon the smallness and, by extent, upon the grandness of phenomena are absolute. It is not possible to go beyond these limits once the observation set is fixed. Analysis and interpretation may impose further limitations even if the sampling aspects of grain are small and the extent is large. Understanding involves rejection of the full set of ways to look at a sampled system, in favor of a powerful subset that allows relevant prediction. It is precisely because of limits of human comprehension that analyses are performed explicitly to remove fine-grained distinctions so that large scaled phenomena may emerge in interpretation. The preliminary sampling aspects of grain and extent in observation sets give the limits of what it is possible to see; within these limits, transformation and analysis further confine what is seen to something commensurate with human comprehension. Furthermore, even with modern computers and a defined system like the game chess, computational limits are reached remarkably quickly (Pattee 1973). In systems where the rules are unknown, such as the interrelationships of the leaves on just one tree, computational limits close in immediately (Weinberg 1975).

Looking In and Out

Now consider the difference between looking in at entities as opposed to looking out at the environment. Looking inward, the observer sees the discreteness of entities (figs. 2, 3, and 4). Looking outward, the observer focuses his attention on the background rather than on any discrete object (figs. 5 and 6). Looking out directs attention at the environment, not the discrete entities.

Koestler (1967) emphasized the part-whole duality of entities in a hierarchical system. He viewed entities as windows of interconnection between their parts and the rest of the universe. Note how, in that conception, the rest of the universe is undifferentiated; it corresponds to our notion of environment. Looking out at the environment, in the present scheme, endeavors to fit the entity of interest into the larger whole. The entity is conceived as a part. By contrast, looking in toward its outer surface, the entity is seen as a whole.

Consider looking in, with an observation set of small extent so that only a single entity can be differentiated (fig. 4). Everything else is considered to be part of the environment. Environment is explicitly not differentiated into entities. It is that "everything else" which can be defined only in terms of its dynamical influence on the structures of definition. Now, increase the extent so that a second entity is detected and seen to be interacting with the first (fig. 3). Now a part of the original set of "environmental influences" can be seen to be interactions between the two entities. If structure is recognized in the environment, then one is no longer looking at environment, but instead, at a pair consisting of the original entity and the new entity which emerged from

the environment. The new structure emerged from the dynamical background as the extent of the observation set is increased. Looking outward focuses on the fact that the original entity, and now the pair of them, is part of a greater whole, as yet structurally undefined, and subject to influences from that context.

To match the part/whole duality of the entities in a hierarchical system, there is a corresponding duality for dynamics. Dynamics link parts to make the whole and deliver the influence of the whole to the parts. Entities sandwiched between the dynamical influences of their environment are in one direction, and the dynamical interaction of their parts are in the other direction.

Structures thus possess two sets of behaviors or processes. One set is directed upward to the next level and pertains to the "part" mode of the structural part/whole duality. The other behavior is directed downward, and is the dynamic that pertains to the "whole" mode of the structural part/whole duality. This downward directed dynamic gives the structure as a whole control over its parts. It is not always immediately apparent to which set (i.e., upward or downward directed) any given behavior belongs. That only emerges when grain and extent are manipulated for several criteria so that dynamics leading to parts can be discriminated from behavior leading to higher levels. It is possible for a given behavior to have aspects that lead upwards and other aspects that lead down, as will be demonstrated later.

Moving through Surfaces

When a surface is viewed from the outside, the separateness of the parts is ordinarily lost (fig. 4 compared to fig. 2). Conversely, when a surface is viewed from the inside, the separate identities of other higher level entities are lost (fig. 2). Distinctions that can be made on one side of the surface cannot be made on the other, because the signal is integrated and filtered out by the surface. The separate parts are merged into the integrated whole (fig. 4) and the other entities are mere-

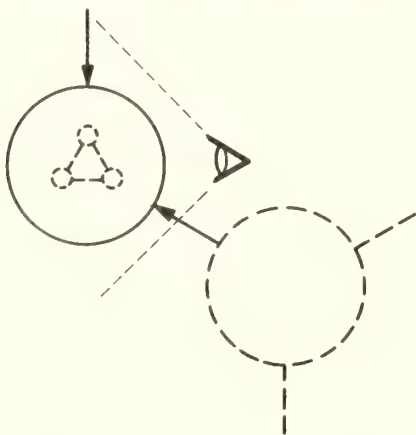


Figure 4.—Seen from outside, the parts are obscured by the intervening surface and the other entity is manifested only as an environmental influence of undefined origin. (The eye indicates the position from which the system is observed.)

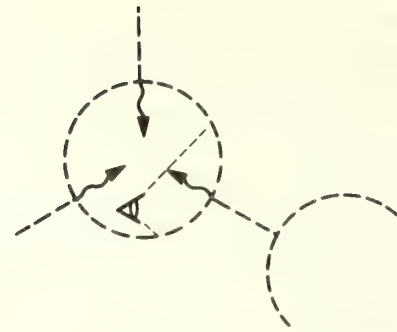


Figure 5.—From inside the surface, looking outward, the observer cannot see the other entity because of the intervening surface. All he can see are the wavy lines which denote environmental influences modified by the surface. (The eye indicates the position from which the system is observed.)

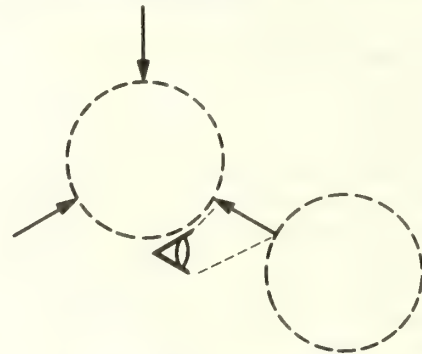


Figure 6.—When the observer looks outward from a surface, he can identify unmodified environmental influences, but he does not have sufficient scope of vision to see the other entity. (The eye indicates the position from which the system is observed.)

ly part of an undifferentiated environmental influence (fig. 5). In both cases, structure on the other side cannot be seen through the surface (Platt 1969). When an observer moves far enough through a surface, the distinctions on the other side become clear. Either formerly obscure parts can be detected (figs. 2, 4, and 5) or separate entities emerge from the environment (figs. 2 to 6).

The way appearances and relationships change as one moves through a surface can be clarified by an example. Species association (Williams and Lambert 1959) is a relative matter, relative particularly to the size of the universe in which the comparison is made (i.e., the extent of the observation set). Consider a two-by-two contingency table for tree species association within a forest. Such a table might well show a negative association between species occurrences, indicating distinct distributions of the species within the forest. The association is negative, because most samples contain either one species or the other, and relatively few contain both.

Now increase the extent of the observation set with additional samples taken in adjacent grasslands. Because neither species appears in these new samples, the number of mutual occurrences does not change. Previously, expectations of mutual occurrence were high, because both species were common in the data set: common species should occur together commonly. As the observation set is extended, the proportion of

samples containing either species becomes smaller. As the species become less common, there should be fewer mutual occurrences, and the observed values move closer to expectations. As a result, the negative correlation disappears. Move out through a surface and the distinction between the species distributions (inferred from the negative correlation) is obscured (fig. 2 compared to fig. 4).

Further expansion of the observation set to include more and more grassland samples makes both species rare, and their mutual occurrences now appear higher than expected. That is, the two species are now very rare and generally would not be expected to occur together at all. However, they still do occur together: now more frequently than one would expect if each were randomly distributed across the entire sampling universe. At this point they become positively associated and are seen as sharing the status of "forest species." Now, positive associations appear among forest species, and negative associations separate the forest species as a group from the grassland species as a group (Beals 1973).

Moving out through the surface of the forest altered what can be observed. Within the forest (fig. 2) one could discriminate between species distributions. Pioneer trees were distinguished from climax trees by negative associations (i.e., if one is present, the other is likely to be absent). As the observation set is expanded, the distinction between species (fig. 4) is lost. Pioneer and climax trees are both forest species, and that common identity begins to emerge. Further expansion of the observation set (fig. 3) makes it impossible to discriminate among tree species, which are now seen together as part of an entity distinguished from a second entity (i.e., grassland species) by negative associations.

Moving Out through a Surface

Movement out through any surface, such as the forest, is achieved through a new observation set which is greater in extent. Usually, it is also more coarse-grained. Coarse grain erects an opaque surface, because it does not allow perception of the smaller entities on the other side of the surface (fig. 4). Movement in through a surface may be achieved by the converse operations, using an observation set which has smaller extent and is also finer grained. The observation set now has a narrower extent, and the observer is trapped within the surface of any entity larger than the extent of the observation set (fig. 2).

Because of the change in grain, surfaces are ordinarily opaque. The only exception is when a new observation set involves only a change in extent. When a higher level emerges by virtue of a simple increase in extent, the smaller entities still may be detectable and are not necessarily obscured by the surface. It is this special case that allows one to tunnel from one level to the next, and to draw direct perceptual links between levels.

Transparent surfaces are crucial for linking levels, but are limited as a way to look at the higher level entity. When a surface is transparent, the new entity is simply

an aggregate. It is being viewed by the same criteria which make the parts interesting objects of study. New properties which might be interesting at the higher level, sometimes called emergent properties, will not ordinarily be seen in this observation set. Higher levels of organization are important precisely because they have properties which are not immediately relevant to the parts. If organisms seen as aggregates of organs and tissues did not also display homeostasis and reproduction, there would be little reason to designate them as special objects of study. It is only when new properties are seen that the differentiation of the higher level entity advances understanding and enriches experience. These properties do not appear unless the criteria for observing the higher level entity differ from those used to study the parts. Thus, the observation sets appropriate for different levels ordinarily differ in criteria. Although there is a special case where surfaces appear transparent, the normal change in observation criteria that occurs as the observer changes his level ensures that the surfaces of most entities are opaque.

Returning through the Surface

Once the interesting properties of the higher level entity are identified, it is often profitable to change grain and extent and move back within the surface. However, now the criteria for observation have changed. For example, "forest" might be identified as a higher level entity in an extensive observation set on tree species. Now the interest is in the forest as an entity that fixes carbon. At this point the focus is on a new property of the forest. The motivation for moving back across the surface of the forest is to identify relationships or interactions (which may amount to mechanisms) operating between the parts, which explain the new property. The surface of the larger entity is transparent under this new criterion, since only extent manipulated and primary production by individual trees within the forest is observed. However, the new observation set on the lower level entities is based on new criteria and is not identical to first observation of this level. In the first observation set, trees were grouped into species categories. Now, when the observer re-enters the forest, entities may be grouped according to whether they are in the canopy or the understory, irrespective of species. New entities, herbaceous plants which were not considered in the original observation set, will also be included.

It is satisfying to the observer if the parts and their interactions in the new observation set are identical to those observed in the original analysis of the trees. In this case he feels confident in the linkage established between the levels. However, in the face of emergent properties, there is the possibility that the parts and processes observed by moving back inside the surface will be somewhat different.

If the same parts and processes cannot be observed as one moves back within the surface, the linkage between levels (i.e., between the new properties of the higher level and the old parts in the original observation

set) remains inferential rather than perceptual, and the surface is opaque. The point of significance here is that there is no reason to expect criteria for observing one level to apply to observing another. The only time a match can be hoped for is when only grain and extent are changed. When criteria of observation change (i.e., when new properties are identified at the higher level) there is no *a priori* reason to believe that the new properties can be reduced to interactions among the old parts. New parts and new processes may be expected. Just because large scale entities remain observable under new criteria (e.g., forest defined by carbon fixation rate as opposed to species composition), there is no need to expect a concomitant mapping (Rosen 1977) of the parts. The large scale entity may be robust (i.e., preserved under different observation criteria), even though the parts needed to explain behavior under the new criteria may change. The result is that trying to link properties of interest at one level to properties of interest at a different level is a difficult process.

Inferring the Whole from the Dynamics of the Parts

Despite the difficulties, ecologists must draw inferences across levels. Therefore, one must analyze what is involved in such inferences. With increase in the extent of an observation set, a surface is reached. At this point, a set of interacting entities have formed a sort of closure, so that they are interacting among themselves with high frequency and show only lower frequency interactions with the undifferentiated environment. The higher level entity has now emerged (fig. 7).

By comparing observation sets on either side of this surface, one can now infer that the entities observed inside the surface indeed are the interacting parts which make up the new whole and can be observed from outside the surface (fig. 7). It is precisely the rapid interactions among the parts which result in the structural integrity of this new whole. The new structure is defined by the dynamics of the parts.

Note here that multiple observation sets are required to draw inferences about linkages between levels. Observation sets that differ in criteria or in both grain

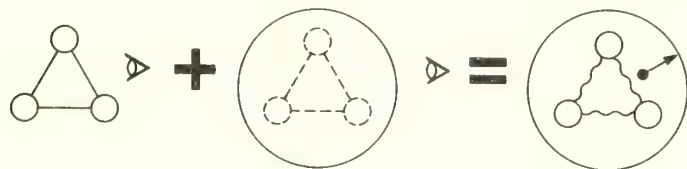


Figure 7.—Drawing inferences about the relationship between parts and wholes. The first observation set sees the collection of parts and their interactions but cannot see the larger whole because of narrow extent. The second observation set uses the same criteria for distinction, but with coarser grain and larger extent. This second set sees the whole but, at best, only a ghost of the parts. Together these two observation sets allow inferences to be drawn on how relationships among the parts lead to the whole. The dot-arrow symbol points to the whole, but the dot is within, because the whole is conceived as being derived from separate parts. The wavy lines denote inferred rather than perceived relationships.

and extent may only be linked by inference, because each is a separate mapping of the world. The closest one can come perceptually to link between levels is a change in extent, with every effort made to keep the grain and criteria for distinction the same. If criteria change, one cannot be sure of correspondence.

Inferring Environmental Filtering

Moving through a surface while focusing attention outward (i.e., on the environment) leads to a completely new situation (figs. 2 to 5). Now inferences are sought about the manner in which the whole modifies the experience of its parts by filtering of environmental influences. Because the focus is not on entities, the required change in observation set can seldom, if ever, be made by a simple change in extent. The situation will ordinarily involve at least two observation sets and an inference drawn from the comparison (fig. 8).

There is a significant difference in the environment viewed from inside (fig. 5) and outside (fig. 3) of the surface. Outside, an undifferentiated background is seen as influence, manifested in the behavior of the whole through its correlation with environmental measurements. Environmental influence on the parts cannot be perceived, because the parts themselves cannot be seen (fig. 3). Inside, one can see environmental signal modified by passage through the surface. Comparing the observation sets one can infer that the whole modifies environmental influences before they operate directly on the parts (fig. 8).

An example here might help clarify the point. Consider diurnal temperature fluctuations and a forest. Outside the forest, temperature fluctuations are quite large. Inside, the biomass of the trees moderates these fluctuations. Forest trees experience cooler temperatures during the day and warmer temperatures at night than a single tree standing alone in a field. The forest tree experiences only the modified influence, and it is beside the point that the night temperature outside the forest is low. Thus, it is by drawing an inference from the observation of the temperature inside and outside the forest that it can be stated that the environmental influence is modified by the forest. Only then can the observer conclude that the temperature difference results from the moderating influence of the forest, which filters the temperature signal from the environment. In general, in order to draw conclusions about the role of the whole in modifying the environment or constraining the parts, a procedure like this must be followed.

Drawing Inferences Versus Changing Extent

Ecologists often draw inferences using observation sets based on different criteria. There is an important difference between crossing a surface by manipulation of grain and extent, and crossing by change of criteria. When grain and extent are changed to give a different pattern but the criteria for distinction are held constant,

When an orderly change has taken place. The parts and whole are linked in the change that took the observer through a surface. When a change occurs by the imposition of different criteria, the observation sets represent different mappings of the world. It may be that there is coherence across the change, and indeed the change does reflect a part/whole relationship, but this is not necessarily the case.

It should be apparent that errors could easily be made whenever the observer unwittingly changes the criteria for significance. A case in point could involve drawing inferences between species composition of a forest and nutrient cycling. Reduction of grain and extent in an observation set on the forest may show the system parts not as species but as functional entities. These entities may be formed by the interaction of soil, water, organic matter, parts of some plants (root hairs), all of some fungi (mycorrhizae), and communities of organisms such as microbes and nematodes that migrate in and out and are not always included in the functional part. The community with its species will not reappear. As a result, inferences drawn between species composition and the components of nutrient cycling must be tenuous, at best.

Often such inferences can be made more explicit by comparing observation sets that differ only in grain and extent. A case in point arises in comparing ordination analyses based on different criteria. Focusing on different phenomena reveals different aspects of the community. Each aspect refers to organismal relationships based on some linking factor such as disturbance, soil moisture, or intensity of competition. Different factors are based on different criteria of observation, and give constellations of species relationships that reflect different scales in time and space.

As an example, it is possible to interpret communities as determined by either competition or environment. By focusing on competition over a narrow range of mesic conditions, environment becomes merely the context within which competition occurs. On a larger geographic scale which includes environmentally stressed sites, one can view environment as the direct cause of species distributions (Allen and Starr 1982). The difference between the two emphases can be seen, for ex-

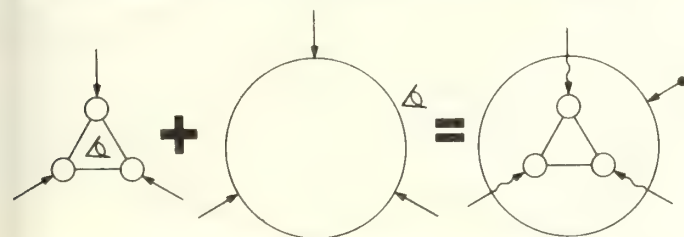


Figure 8.—Drawing inferences about environment based on two observation sets. The first observation set sees only the parts and their immediate environmental influences. The second observation set considers the whole as itself a part of some undifferentiated higher level. Together, these two observation sites allow inferences to be drawn about how the whole ameliorates the environmental experience of the parts. The dot-arrow symbol points to the whole and the dot is outside since the whole is conceived as a modifier of the environmental influence coming from the outside. The wavy lines denote inferred, not perceived, relationships.

ample, in the way that the tolerant, poor competitors (i.e., losers in one observation set) occupy stressed sites successfully (i.e., winners in the other observation set). Notice how it is difficult to hold these two concepts of community at the same time; for environmental stress is the frame in one, whereas competition is the frame in the other. Furthermore, competition is explicitly irrelevant in the stress frame. Putting it another way, a view that focuses on one set of phenomena cannot give a perfect account of a system if the interest is in some different set of phenomena.

To look at a specific case, Loucks (1962) performed ordinations of forests in New Brunswick by two different criteria. One was a Bray and Curtis (1957) ordination of stand species composition. The other was based on scalars of environmental gradients. This is a clear case of change of criteria. Because of this, Loucks was forced into an extended and deeply inferential argument to relate the results of the two ordinations.

The difference between the ordination results was great in that the moisture gradient curved around in the vegetation analysis. Black spruce and cedar were positioned together in the vegetation ordination at the ends of the distorted moisture gradient. In the environmental ordination, the moisture gradient must necessarily be straight, and black spruce and cedar are bimodally distributed, appearing at either end in very moist or very dry sites.

While Loucks was forced to explain these changes indirectly, he recognized that a series of observation sets of increasing extent would be a more direct approach:

“The data for black spruce suggest that if the samples in the lowest [stressed] range of the Nutrient scalar were considered alone, black spruce is not bimodal. It becomes so only when considered with preponderance of other communities that develop at higher levels of the Nutrient scalar; these nutrient levels occur only on intermediate moisture positions.” (Loucks 1962.)

If he had begun with the low nutrient sites and expanded the extent to include more and more mesic sites, he would have seen black spruce and cedar change in an orderly fashion. Both low nutrient status and wet/dry extremes of the moisture gradient represent environmental stress. At the extremes, abiotic stress allows survival of the tolerant in a circumstance where competition is unimportant. Black spruce and cedar would have become rare as the number of mesic sites increased, because neither of them do well under mesic conditions, where competition with other species is important. Then the fine-grained concept (i.e., structured by competition) and the coarse-grained concept (i.e., structured by environment) could have been directly related through a simple change of grain and extent.

Correct and Incorrect Linkages

At this point ecologists can begin to identify the types of error they encounter when endeavoring to link levels of organization. Some rules and warning are already

part of ecological practice, having emerged from the exercise of common sense. Even so, there is something to be said for a scheme that derives from general principles instead of common practice. The former would be a general prescriptive scheme, the latter merely local and descriptive.

Linking Levels through Phenomena

Any scientific investigation starts by designating the entities one chooses to discriminate. The entities are structural and arise from the criteria for recognizing entities in an observation set. For example, one can choose to study individual organisms. Then he observes that the individuals demonstrate behavior (i.e., they can change through time). Once the entities are fixed, the observer has no choice as to whether or not his measuring device detects change. In this sense, the behavior of the individuals is forced on the observer.

Although the dynamics of the entities are forced on the observer, he must still make a second, observer-dependent choice concerning which specific dynamics he will consider to be of importance. The observer must enter the process again and decide the particular changes of state he will select as significant. The changes he selects constitute the "phenomena" of interest. Thus phenomena are dynamical behavior but are quite distinct from the raw dynamics that are imposed on the observer when he infers differentials for the measured states of the structure of interest. The raw dynamics are objective and imposed on the observer, while the dynamic which is a phenomenon is the special subjectively chosen subset which represents only the dynamics asserted to be interesting.

Observation, therefore, depends on two distinct choices separated by dynamics. The steps involved in setting up any observation set are (1) the choice of the level of interest and the entities or structures at the level, (2) the development of a means to observe changes in these entities, and (3) the choice of which changes will be considered significant (Rosen 1977). The observer decides about both entities and phenomena even though the dynamics are imposed on him.

Phenomena form crucial links between levels. Consider observations made on individual organisms through time (fig. 9). Among other things, the observer notices that eventually each of the individuals ceases to function. He decides this change of state is interesting, and "death" is established as the phenomenon (fig. 9). By increasing the extent of our observation set to include the death of many individuals it is possible to calculate a death rate.

The dynamic now links the observations to a higher structural level since death rate is a behavioral dynamic of the population (fig. 9). The individual and the population are linked through their dynamics by having a phenomenon, death, in common. Whenever a phenomenon is significant at two levels, it can be used to link the levels. The link is made perceptually since it only involves changing the extent of the data set on dynamics. This is another example of the fact that a direct or perceptual

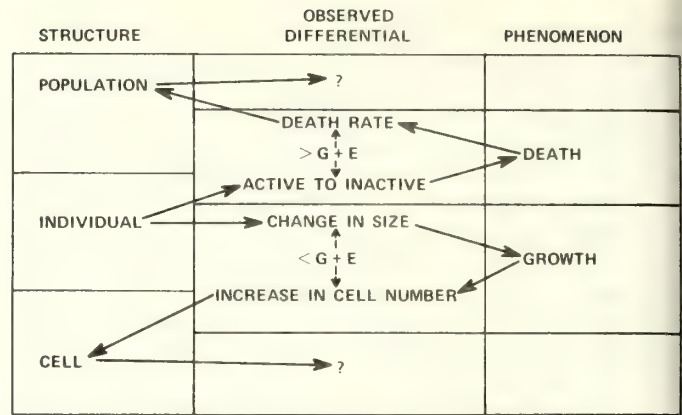


Figure 9.—Entities at structural levels above and below the individual are linked by first observing a differential (i.e., a change in state), then denoting an appropriate phenomenon, and finally observing again with modified grain and extent to observe a new behavior that links the phenomenon to the other level.

linkage between levels can only be made by a simple change in grain and extent while maintaining the same criterion of distinction.

An analogous path can be followed to connect the organism to lower levels (fig. 9). Once again observations will be made on the individuals, but now special attention will be given to change in size for each organism. Thus, "growth" is selected as the phenomenon. If the extent of the observation set is maintained, but a much finer grain is selected, changes in the number of cells might be seen (fig. 9). This leads to a lower structural level, because change in number is a dynamic definable on the entity, "cell." Thus, once again levels have been linked by a change in grain and extent using a phenomenon that they have in common. Note, however, that we could choose the phenomenon "growth," see trees grow, expand extent to see many trees growing, and then infer growth as an internal dynamic of a larger structure, namely forest.

Of course, it is possible to explain the phenomenon of growth in other ways. One might decide to examine caloric inputs, arriving at growth as the net difference. This approach is certainly legitimate, but, because of the change in criteria, it is unlikely that cells would be discovered as a lower level entity. The change in criterion would destroy the ability to link these levels considered above.

This approach for linking levels may seem pedantic and overdrawn. However, the necessity for the distinctions can only be appreciated when we see the errors which can be made when the linkage is made on less rigorous grounds.

Error in Linking Levels

The level to which the link is made may change depending on the phenomenon chosen. In the end, different levels may be linked than those the observer had in mind because the phenomenon chosen had different consequences than those he intended. The starting point for this example is the population, and the dynamic involves

aging and eating. If the behavior, eating, is seen to be associated with the phenomenon, pollination, then an expanded conservation set could lead to an upper level entity called "guild" (fig. 10). Alternatively, given the same structure and behavior, if the phenomenon is recognized as primary consumption, then an increase in extent of observation set would lead to "trophic level." As a further alternative, recognition of the behavior as an interspecific relationship might lead one up the "community" (fig. 10). Thus, the linkages depend on the phenomenon, not just the raw observed changes in state. Similarly, the levels which the ecologist links may change, if he changes the dynamics which he observes. Consider figure 9 once again; but now observe whether or not individuals mate with each other. The relevant phenomenon might now be constancy of mating among individuals of a similar type. Now a change in extent could not lead to the population or community, but to the taxonomic species as the next higher level.

These examples illustrate a problem commonly found in linking levels in ecology. Given the definition of level and phenomenon, it is clear from figure 10 that there are no absolute levels of organization, independent of the observer. There is no Platonic Chain of Being. Given prior choice of structure defining the starting level, it is the choice of phenomenon that determines what is the next level in the hierarchy, whether it is the next level up or down. The phenomenon is chosen by the observer, not imposed by the external world; and it is the phenomena that both explain the workings of higher levels and describe the role of lower levels. Thus, the analysis presented here reveals that any attempt to find the true ecological hierarchy (e.g., MacMahon et al. 1981) is founded on an inadequate epistemological base and must of necessity fail. Intermediate or alternative levels always can be located by a change of phenomenon. When one moves up and down from the starting point of choice, the other levels are not fixed by what other investigators, with other observation sets, might choose as their starting points. Thus, the first problem with this analysis is the widespread practice of choosing the levels in the hierarchy *a priori*. The higher and lower levels must be revealed to the observer by a

change in grain and extent with the entities needed to explain the mechanics (lower) and function (higher) of the chosen phenomenon.

This problem often arises in linking levels which are widely separated. Allen and Starr (1982) note that it becomes much harder to connect levels directly when there are intervening levels which are relevant to the chosen phenomenon but ignored. A case in point would involve explaining environmental control of phytoplankton communities by recourse to cell physiology and uptake rates of nutrients. Allen et al. (1977) suggest that the intervening levels of species, guilds, and strategies (Allen and Koonce 1973) attenuate and confound the linkage. Difficulty arises because the levels of observation are too far apart and articulation is lost. The levels of organization were imposed instead of being allowed to emerge from observations.

A similar problem arises in attempts to link ecosystems to communities or populations (fig. 11). Once again, the levels are prescribed, and the linkage is assumed. It is true that ecosystems have populations in them, but this "observation" actually involves a number of observation sets, based on very different criteria. In this report, it has been demonstrated that such a specification of the complex problem is inadequate, and depends upon insufficient evidence to establish the linkage. As a result, there is an epistemological problem with defining the ecosystems as composed of plant and animal populations and their environment.

To link ecosystems and populations, it is necessary to establish common phenomena and show that the observation sets that lead upward to the ecosystem and downward to the population involve a change of grain and extent but not change in criteria. In fact, it is possible to make this connection for some phenomena but not for others (fig. 11). Consider, for example, primary production. Here, a simple change of grain and extent will reveal that plant populations, and nothing else, are involved in this dynamic. However, other ecosystem phenomena, such as nutrient retention, do not provide adequate linkages. It was previously identified how a relevant component here, the rhizosphere, is a strange mixture of organism wholes and parts. The problem is that the dynamic does not result only from interactions among biotic populations. Nutrient retention may be in part biotic (tree boles), it may be abiotic (soil organic matter), or it may be due to a complex interaction. In this case, the ecosystem dynamic will not emerge from any observation set on the populations and their interactions. There is no simple increase in grain and extent that takes the population observations to nutrient retention dynamics of the ecosystem. The links only occur when an ecosystem phenomenon is given account by a single population or an aggregate of populations.

Another common error in linking ecological levels results from ambiguity in the words used to delineate a phenomenon. For example, the word "competition" implies a link between individuals and populations. However, the meaning to the word is very level-dependent. As Harper (1967) points out, individual competition is commonly between the mature of one species

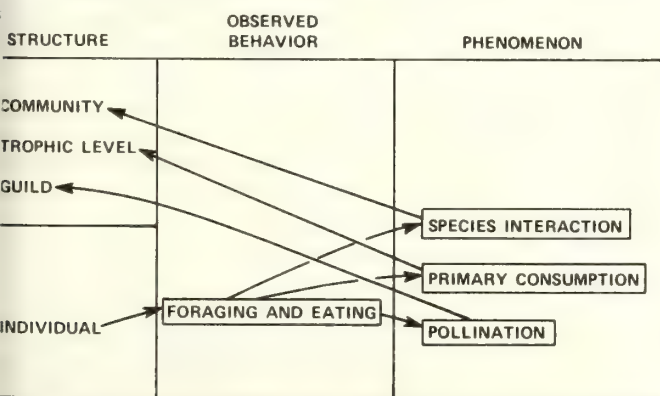


Figure 10.—The structures at the individual level are observed to change state and so exhibit behavior. Three different phenomena can be chosen on the same observation set and each links the individual level with a different upper level structure.

and the juveniles of another. Therefore, there is much confounding of neighborhood and population competition. Although the treatment of competition as something very local permeates much of J. L. Harper's earlier work, "Neighborhood competition" did not even arise as a specific technical term for individual to individual competition until recently (Mack and Harper 1977). The taxonomy of the individuals in neighborhood competition is usually unhelpful in explaining the observation since size and maturity are the determining factors. At the population level, "competition" refers to interactions among populations. Thus, if the observation set used to detect neighborhood competition does not contain information on the species, it cannot be changed by grain and extent to detect the competition which is of interest at the population level. If the observation set that detects population competition does not (as most do not) contain size hierarchy information, then a narrowing of grain and extent will not lead to neighborhood competition. The relationship between the two types of competition is by metaphor or, at best, analogy. The mistake is to assume that they are homologous.

Neighborhood competition viewed as resource capture does lead to populations seen in terms of resource base, because behavior of populations with respect to resource base is a simple extension of neighborhood resource capture, that extension being achieved through manipulation of only grain and extent. It is a population behavior that may be seen as directed downward. Population competition, however, involves behavior that is most readily seen as linking populations to make higher, not lower, hierarchical levels.

Similar ambiguities arise with the word "stability" used to link ecosystems and populations. At the ecosystem level, stability may refer to the constancy of a function, such as a primary production. At the population or community level, stability may refer to the fact that all of the populations are still there following a disturbance. However, it is quite possible the primary pro-

duction has remained constant following a disturbance precisely because of species replacement resulting from resource competition. One population has disappeared and another has expanded to take over its function. Thus, the system can be considered simultaneously a stable and unstable depending on the level of interest. As a result, the phenomenon "stability" is a poor candidate for linking the levels. Simply because the same word is used for phenomena on two levels does not insure adequate linkage. One must be certain that the criteria have not changed even though the word has remained the same.

Summary: General Principles for Linking Levels

The following summarizes these analyses in a set of general principles.

1. The level at which an inquiry begins is arbitrary. The observer chooses the entities on which he will focus and they are differentiated by observer-defined criteria. Effective criteria emphasize surfaces that (1) coincide with significant changes in rates of interaction, and (2) can be detected in different observation sets (i.e., are robust under transformation, as forest edges that coincide for change in both temperature and biomass).
2. A scientific description of the level chosen for study requires explicit recognition of part/whole duality (Koestler 1967). The entity of interest will consist of parts (i.e., lower level entities) which it constrains and contains. At the same time, the entity of interest must be seen as part of a greater whole although this may be described in undifferentiated terms as its environment. To describe the entity as both a whole composed of parts and as a part of a greater whole will ordinarily require drawing inferences based on different observation sets; and the inferences will only be validly grounded on a perceptual basis if the criteria for significance have not changed between the observation sets. To move upward in the hierarchy will require an observation set with sufficient extent that it includes a number of entities and their interactions. To move downward requires an observation set of sufficiently fine grain that the individual parts and their interactions can be observed.
3. Once the observer begins to make observations on the entities, he can detect changes which correspond to their behavior unique to that level. A full description of dynamics, like structure, is also dual, and both delivers constraints downward to parts, as well as showing how the entity responds upwards to the greater whole of which it is a part. To understand both the upward and downward aspects of dynamics will ordinarily require inferences based on multiple observation sets.
4. Following observation of dynamics, a further observer-dependent choice must be made. This arbitrary decision involves the aspect of dynamics which will be given special significance and called

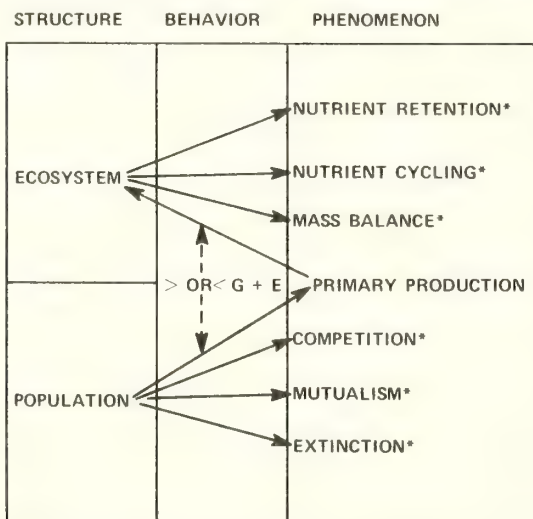


Figure 11.—Ecosystems can be linked to population, but only if a phenomenon can be identified that is common to both, such as primary production. The asterisks denote phenomena that are not common to both levels and cannot serve to link the levels.

the "phenomenon" of interest. The choice of phenomena will then determine the higher and lower-level entities with which we can establish linkages.

Dynamic linkages between levels are established through phenomena. If the phenomenon in combination with a change of grain and/or extent can be established as interesting at both higher and lower structural levels, and if it can be related to each of these levels through observation sets on dynamics that differ only in extent or grain, then the linkage is justified. Care must be taken that the word used to describe the phenomenon has the same meaning on both levels.

Linkages between levels using only a change in grain and extent are crucial for established unequivocal or at least justified assertions of relationship. Only one phenomenon should be involved with only one set of criteria for observation. The relationship is simple because upper levels here are only aggregates of lower levels.

The simplicity of relationships so defined severely limits what insights can be derived. Fortunately levels which emerge from such simple relationships may persist when criteria for observing them are changed. Once they are found, emerging levels may be robust under transformation. Reverse manipulations of grain and extent using these new criteria do not usually lead back to the original level because a new phenomenon associated with the new criteria has become involved. Explanations of the new phenomenon do not return to the original level of concern but to a new level defined by the new criterion for observation.

From the above, the relationship between levels can be explained by alternative criteria (e.g., the relationship of a forest to alternative lower levels is complex: First, move from one lower level to a forest using one criterion, increasing the grain and extent; next, shift the criteria for defining a forest; finally, reduce to the alternative lower level by a reduction in grain and extent of the second criteria).

Attempts to link prescribed levels are difficult because the linking phenomena are undefined, and it may not be possible to find them under any observation set.

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This report clarifies the role of the observer and what he observes as an aid to ecological research and natural resource management. It describes what is involved in observing complex natural systems, and finally summarizes, from these, the important principles in linking levels of natural systems that emerge.

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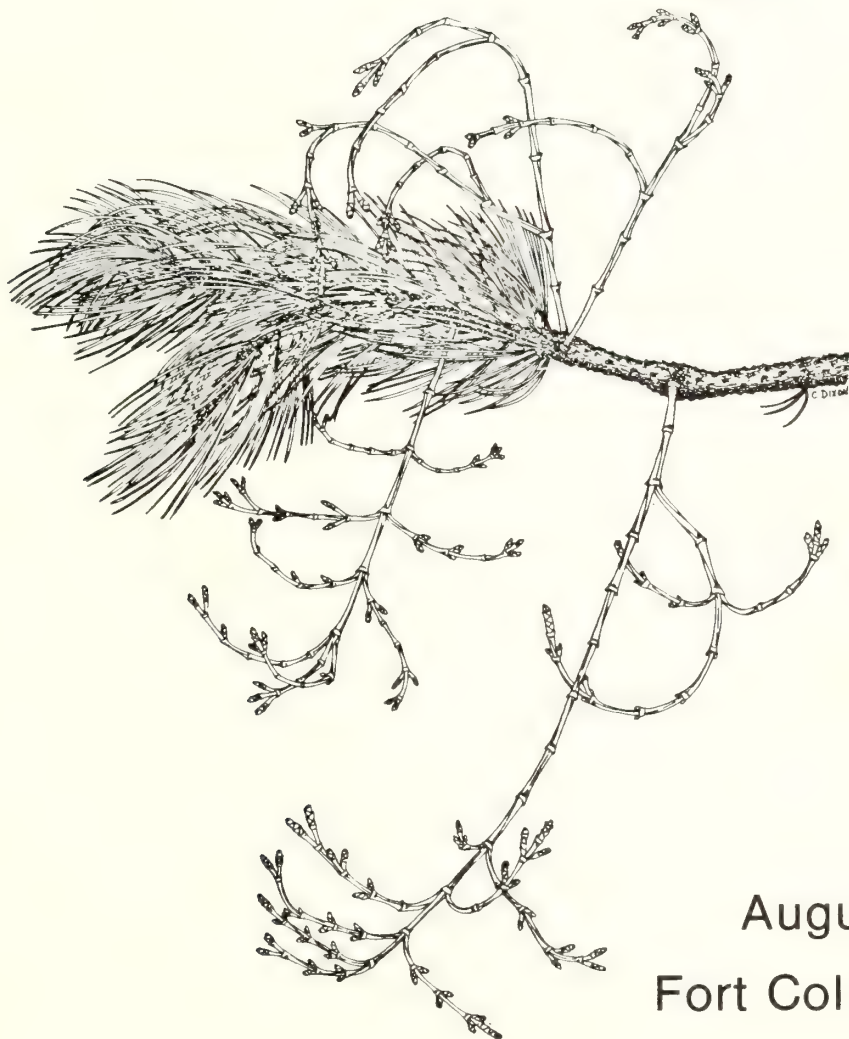
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General Technical
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Biology of Dwarf Mistletoes:

Proceedings of the Symposium



August 8, 1984
Fort Collins, Colorado

Preface

"So much has already been written on this genus of the Loranthaceae that many readers...will no doubt be surprised that there should be anything new to be said on the subject." This profoundly non-prophetic statement was written by T. Johnson in an article on Arceuthobium oxycedri in the Annals of Botany in 1888. Indeed, much more has been written on the subject in the ensuing century (at least 3,500 references) but much more remains to be learned about this fascinating genus, the most advanced of the mistletoes.

The dwarf mistletoes are the most damaging group of parasitic seed plants in North America. They parasitize several species of conifers, including the most important commercial timber trees. The group is also very interesting from a biological standpoint because of the long period of co-evolution of host and parasite. The dwarf mistletoes are extremely reduced morphologically, very host specific, and are nearly holo-parasitic. The dwarf mistletoes were the subject of a USDA Forest Service-sponsored symposium in 1978, but that symposium focused on control through forest management, not basic biology. The National

Institute of Biological Sciences meeting at Colorado State University, Fort Collins, provided an opportunity for biologists from various disciplines to meet and discuss the biology of the dwarf mistletoes.

Rapid publication of these proceedings was due largely to the excellent efforts of the authors (and their typists!) in preparing camera-ready manuscripts. Since papers are being printed as received, each contributor is responsible for the accuracy of his or her paper; opinions expressed by the authors may not necessarily reflect the policy of the U.S. Department of Agriculture.

Many people contributed to the success of the symposium. The original suggestion to hold the symposium was made by Clyde L. Calvin, of Portland State University. We thank the many scientists who kindly provided reviews of manuscripts for these proceedings: Neil A. Anderson, Clyde L. Calvin, M. Thomas Conkle, William B. Critchfield, Leanne Egeland, Carl Eide, George T. Ferrell, F. Thomas Ledig, Arthur H. McCain, Michael E. Ostry, and Richard S. Smith. R. H. Hamre compiled the proceedings for publications.

Cover: A recently described dwarf mistletoe, Arceuthobium pendens, a rare parasite of pinyons in Mexico (see p. 5). Drawing by Christine Dixon.

BIOLOGY OF DWARF MISTLETOES: PROCEEDINGS OF THE SYMPOSIUM

August 8, 1984
Colorado State University,
Fort Collins

Frank G. Hawksworth and Robert F. Scharpf
Technical Coordinators

Sponsored by:

Rocky Mountain and Pacific Southwest Forest and Range Experiment Stations
USDA Forest Service

Botanical Society of America

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Contents

Page

INTRODUCTION

Dwarf Mistletoes: Insidious Pests of North American Conifers. <i>Ed F. Wicker</i>	1
--	---

BIOSYSTEMATICS, HOSTS, AND DISTRIBUTION

Biology and Classification of <i>Arceuthobium</i> : an update. <i>Frank G. Hawksworth and Delbert Wiens</i>	2
<i>Arceuthobium</i> and its Hosts in Southwestern China. <i>Kiu Hua-sing</i>	18
Biosystematic and Evolutionary Relationships among Selected Taxa of <i>Arceuthobium</i> . <i>Daniel L. Nickrent, Sheldon I. Guttman, and W. Hardy Eshbaugh</i>	20
Genetic Variability in the Dwarf Mistletoes <i>Arceuthobium vaginatum</i> subsp. <i>cryptopodum</i> and <i>A. americanum</i> on their Primary and Secondary Hosts. <i>Yan B. Linhart</i>	36

ANATOMY, PHYSIOLOGY, AND RESISTANCE

The Anatomy and Morphology of the Endophytic System of <i>Arceuthobium</i> spp. <i>M. Carol Alosi and Clyde L. Calvin</i>	40
Altered Concentrations of Abscissic Acid, Indole-3-Acetic Acid, and Zeatin Riboside associated with Eastern Dwarf Mistletoe Infections on Black Spruce. <i>William H. Livingston, Mark L. Brenner, and Robert A. Blanchette</i>	53
Water Metabolism and Seedling Photosynthesis in Dwarf Mistletoes. <i>Richard D. Tocher, Steven W. Gustafson, and Donald M. Knutson</i>	62
Host Resistance to Dwarf Mistletoes. <i>Robert F. Scharpf</i>	70

POPULATION DYNAMICS

Seed Development, Germination Behavior, and Infection Characteristics of Several Species of <i>Arceuthobium</i> . <i>Donald M. Knutson</i>	77
The Pollination Biology of <i>Arceuthobium americanum</i> in Manitoba. <i>Jeannie Gilbert and David Punter</i>	85
Insect-Dwarf Mistletoe Associations: an Update. <i>Robert E. Stevens and Frank G. Hawksworth</i>	94
Animal Vectors of Dwarf Mistletoe, with Special Reference to <i>Arceuthobium americanum</i> on Lodgepole Pine. <i>Thomas H. Nicholls, Frank G. Hawksworth, and Laura M. Merrill</i>	102

ECOLOGY

Relationships between Dwarf Mistletoes and Habitat Types in Western Coniferous Forests. <i>Robert L. Mathiasen and Elizabeth A. Blake</i>	111
The Effect of Dwarf Mistletoe on Forest Community Ecology. <i>Robert O. Tinnin</i>	117
Ecological Interrelationships of Dwarf Mistletoe and Fire in Lodgepole Pine Forests. <i>G. Thomas Zimmerman and Richard D. Laven</i>	123

Dwarf Mistletoes: Insidious Pests of North American Conifers

Ed F. Wicker¹

Dwarf mistletoes are parasitic seed plants of the genus *Arceuthobium*. Members of this genus have not attained the symbolic or historical significance of other taxa of the family Viscaceae but they excel as destructive pathogens of forest trees in the family Pinaceae. Several species are native to North America. Although genesis of the taxa likely surpasses that of their hosts in antiquity, the two have co-evolved over several million years. The genus reaches its greatest degree of diversity in western North America.

Recorded observations on the parasitic behavior of mistletoes date to Theophrastus, 305 B.C. (Gill 1953). The earliest written record of dwarf mistletoe discovered so far was that of Clusius in 1601 from southern Europe (Hawksworth 1978). The parasite was not reported from North America until the early 1800's. For the next 100 years or so, interest on these plants was driven mainly by botanical curiosity.

Although the importance of dwarf mistletoes as destructive pathogens in western coniferous forests was documented in the early part of the twentieth century (Weir 1916a, b), they remain a most important forest disease problem. Our best estimate for annual losses of timber products attributable to dwarf mistletoes in the western United States now stands at 3.3 billion board feet. On a regional basis, it has been estimated that 50 percent of the lodgepole pine and Douglas-fir forest and 35 percent of the ponderosa pine forest of the Central and Southern Rockies are affected by dwarf mistletoes. Some stands are so severely damaged that they are producing at less than 1/3 potential. Such production certainly cannot be considered economically feasible management. Estimates of annual losses of timber products in the Northern Rockies attributed to dwarf mistletoes exceed those for the Central and

Southern Rockies. Possible losses in tree seed production, product quality, predisposition to other pests, recreation and aesthetic values, and wildlife habitat have not been reported.

Silvicultural practices can be used to reduce intensity of dwarf mistletoe to non-pest levels. Such practices are being implemented on millions of acres of commercial forest lands in the western United States, and good progress is being made in reducing productivity losses to dwarf mistletoes. This control program is in constant need of refinement to stay in step with changing needs and demands of society. Increased knowledge of the biology and ecology of the pest will prove invaluable in meeting these demands for change in the control program.

I would like to close with a word of caution. We have a long way to go in this war with dwarf mistletoe. Silvicultural controls take time, and that time can work both for and against us. Dwarf mistletoe is a slow, insidious pest that fights a war of attrition. It wears down our interest, the visibility of our efforts, and thus the financial support for our control programs. The best insurance to avoid this happening is for research to (1) rapidly develop the capability to accurately quantify production losses caused by dwarf mistletoe, and (2) respond quickly to changing economic and social demands that may require changes in on-going control efforts.

These needs are long-standing, and so far research has been slow to respond. Consequently, we are paying the price in terms of dwindling support. It is imperative that we look on this symposium on biology of dwarf mistletoes as a building block in our fight to achieve effective, long-term control of an exceedingly costly, tenacious forest pest!

¹ Assistant Director for Research, Rocky Mountain Forest and Range Experiment Station, USDA Forest Service, Fort Collins, Colorado

Biology and Classification of *Arceuthobium*: an update¹

Frank G. Hawksworth and Delbert Wiens²

Abstract.--*Arceuthobium* is the only mistletoe genus that occurs in both the New and Old Worlds. In our 1972 monograph, we recognized 32 taxa; 28 in the New World and 4 in the Old. Since then, 9 new taxa have been described or recognized; 5 in the New World and 4 in the Old. Most of the new taxa in the New World are on *Pinus*: *A. aureum* ssp. *aureum* in Guatemala and Belize; *A. aureum* ssp. *peterstonii* in southern Mexico; *A. globosum* ssp. *grandicaule* in Mexico and Guatemala, and *A. pendens* in central Mexico. The most surprising is a new species, *A. cubense*, on *Podocarpus* in eastern Cuba, the first report of a host of *Arceuthobium* in the Podocarpaceae. This is so exceptional that verification is needed. In the Old World, the recently described or recognized taxa are: *A. azoricum* on *Juniperus* in the Azores; *A. juniperi-procerae* on *Juniperus* in Ethiopia and Kenya; *A. tibetense* on *Abies* in southwestern China, and *A. pini* var. *sichuanense* on *Picea* in southwestern China. The greatest increase in the number of known taxa since 1972 has been in China (from 2 to 6), Guatemala (2 to 5), and Mexico (16 to 19). *Arceuthobium* is reported for the first time in El Salvador and Cuba. *Pinus* is the primary host of the genus (25 of 41 taxa), but for only 2 of the 8 Old World taxa.

Introduction

Arceuthobium is the only mistletoe genus that occurs in both the eastern and western hemispheres. The first report of dwarf mistletoe was by Clusius (1576), who described "*Viscum oxycedri*" on junipers in the Mediterranean area. The first *Arceuthobium* in the New World was described by Willdenow, as "*Viscum vaginatum*," from central Mexico in 1806. *Arceuthobium* was established as a separate genus by Marschall von Bieberstein in 1819. Details on the taxonomic history of the genus are given by Hawksworth and Wiens (1972). Much of the early literature on the genus was taxonomic, although some pioneer forest pathologists, such as Drs. J. R. Weir and L. S. Gill recognized the significant pathological effects caused by these parasites.

The dwarf mistletoes, because of their unique biology and great economic importance, are receiving increasing attention in the literature. In the latest edition of our FAMULUS information retrieval system of world mistletoe literature (Scharpf et al. 1976), we have nearly 3500 titles on *Arceuthobium*. During the first half of the 20th century, there were only 10 publications per year on the genus.

¹Paper presented at the Symposium on Biology of Dwarf Mistletoes, in conjunction with the A.I.B.S. Meetings, August 8, 1984, Fort Collins, Colorado.

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Since 1950, however, the increase has been dramatic:

Dates	Number of <i>Arceuthobium</i> publications/year
1950-1954	26
1955-1959	37
1960-1964	57
1965-1969	81
1970-1974	112
1975-1979	119

The number of publications appearing in the early 1980's indicates that this increasing trend is continuing.

Little taxonomic research on the genus has been undertaken since our 1972 monograph. Crawford and Hawksworth (1979) examined the flavanoid compounds from 36 taxa. The flavonoid chemistry of the genus is rather uniform, all taxa producing 3-O-glucosides of the flavonols quercetin and myricetin. No infraspecific chemical variation was encountered, and, in those instances where subspecific taxa are recognized, their chemistry was uniform. At the subgeneric level, members of subgenus *Arceuthobium* synthesize primarily glucosides, whereas galactosides are more common in subgenus *Vaginata*. In two of the four Old World species of subgenus *Arceuthobium* (*A. juniperi-procerae* and *A. oxycedri*) only myricetin 3-O-glucoside was detected. There are no absolute flavonoid differences between subgenera, sections, or series. Flavonoids, however, are useful in several instances at the species level. In several cases, chemical data lend support to the

Table 1.--Synopsis of the genus *Arceuthobium*.

I. Subgenus *Vaginata* Hawksw. & Wiens

A. Section *Vaginata*

1. *A. aureum* Hawksw. & Wiens ssp. *aureum*
2. *A. aureum* ssp. *petersonii* Hawksw. & Wiens
3. *A. gillii* Hawksw. & Wiens ssp. *gillii*
4. *A. gillii* ssp. *nigrum* Hawksw. & Wiens
5. *A. globosum* Hawksw. & Wiens ssp. *globosum*
6. *A. globosum* ssp. *grandicaule* Hawksw. & Wiens
7. *A. vaginatum* (Willd.) Presl ssp. *vaginatum*
8. *A. vaginatum* ssp. *cryptopodum* (Engelm.) Hawksw. & Wiens
9. *A. vaginatum* ssp. *durangense* Hawksw. & Wiens

B. Section *Campylopoda* Hawksw. & Wiens

a. Series *Campylopoda*

10. *A. abietinum* (Engelm.) Hawksw. & Wiens f. sp. *concoloris* Hawksw. & Wiens
11. *A. abietinum* (Engelm.) Hawksw. & Wiens f. sp. *magnificae* Hawksw. & Wiens
12. *A. apachecum* Hawksw. & Wiens
13. *A. blumeri* A. Nels.
14. *A. californicum* Hawksw. & Wiens
15. *A. campylopodum* Engelm.
16. *A. cyanocarpum* Coulter & A. Nels.
17. *A. divaricatum* Engelm.
18. *A. guatemalense* Hawksw. & Wiens
19. *A. laricis* (Piper) St. John
20. *A. microcarpum* (Engelm.) Hawksw. & Wiens
21. *A. occidentale* Engelm.
22. *A. pendens* Hawksw. & Wiens
23. *A. tsugense* (Rosendahl) G. N. Jones
Hemlock race
Shore pine race

b. Series *Rubra* Hawksw. & Wiens

24. *A. bicarinatum* Urban
25. *A. hondurensense* Hawksw. & Wiens
26. *A. rubrum* Hawksw. & Wiens

c. Series *Stricta* Hawksw. & Wiens

27. *A. strictum* Hawksw. & Wiens

C. Section *Minuta* Hawksw. & Wiens

28. *A. douglasii* Engelm.
29. *A. pusillum* Peck

II. Subgenus *Arceuthobium* (No sections designated.)

New World Species

30. *A. abietis-religiosae* Heil
31. *A. americanum* Nutt. ex Engelm.
32. *A. verticilliflorum* Engelm.

Old World Species

33. *A. azoricum* Wiens & Hawksw.
34. *A. chinense* Lecomte
35. *A. minutissimum* Hook.
36. *A. juniperi-procerae* Chiov.
37. *A. oxycedri* (DC.) M. Bieb.
38. *A. pini* Hawksw. & Wiens var. *pini*
39. *A. pini* var. *sichuanense* H. S. Kiu
40. *A. tibetense* H. S. Kiu & W. Ren

III. Status unknown

41. *A. cubense* Leiva & Bisse

recognition of species that in the past have been considered doubtfully distinct on the basis of morphology: *A. apachecum*, *A. blumeri*, *A. cyanocarpum*, *A. californicum*, and *A. microcarpum*. But, the flavonol chemistry is identical in other closely related species such as *A. campylopodum* and *A. occidentale*.

Arceuthobium has been separated into two subgenera based primarily on branching patterns: verticillate in subgenus *Arceuthobium* and flabellate in subgenus *Vaginatum* (Hawksworth and Wiens 1972). Mark and Hawksworth (1981) studied two California members of subgenus *Vaginatum* (*A. occidentale* and *A. campylopodum*) and showed that they exhibited limited (average less than 5%) verticillate branching, in addition to the predominate flabellate type. Presence of flabellate branching, rather than absence of verticillate branching, is thus a better criterion for distinguishing subgenus *Vaginatum*. Subgenus *Arceuthobium* is apparently exclusively verticillate.

Hawksworth (1982) has published a taxonomic summary of the genus in Mexico and Central America, along with lists of hosts and distribution maps. Barlow (1983) summarized the biogeography of the genus.

In our 1972 monograph (Hawksworth and Wiens 1972), we recognized 32 taxa in *Arceuthobium*; 28 in the New World and 4 in the Old. Since then, 9 new taxa have been recognized or described: 5 in the New World and 4 in the Old.

NEW TAXA SINCE 1972

New World

In our 1972 paper, we suggested that "*Arceuthobium globosum*" might be divisible into other taxa. Subsequent field studies in Mexico and Guatemala show that this is indeed the case, and we now recognize this complex as consisting of at least 2 species, with 2 subspecies each: *A. globosum* (subsp. *globosum* and *grandicaule*), and *A. aureum* (subsp. *aureum* and *petersonii*) (Hawksworth and Wiens 1977).

1. *ARCEUTHOBIUM GLOBOSUM* subsp. *GRANDICAULE*.³ This subspecies is widespread in central Mexico and in the highlands of western Guatemala on at least 10 species of pines (fig. 1). It is the largest *Arceuthobium*, with shoots up to 70 cm tall and 5 cm in diameter at the base. It frequently sprouts from the trunks of pines.

2. *ARCEUTHOBIUM AUREUM* subsp. *AUREUM*. This species occurs on pines in low elevations (900-2000 m.) in Guatemala and Belize (fig. 2). It is apparently unique among the New World dwarf mistletoes in that it flowers and fruits continuously throughout the year. Like *A. globosum* subsp. *globosum* in northern Mexico, this taxon does not induce witches' broom formation.

³Authorities are given in Table 1.

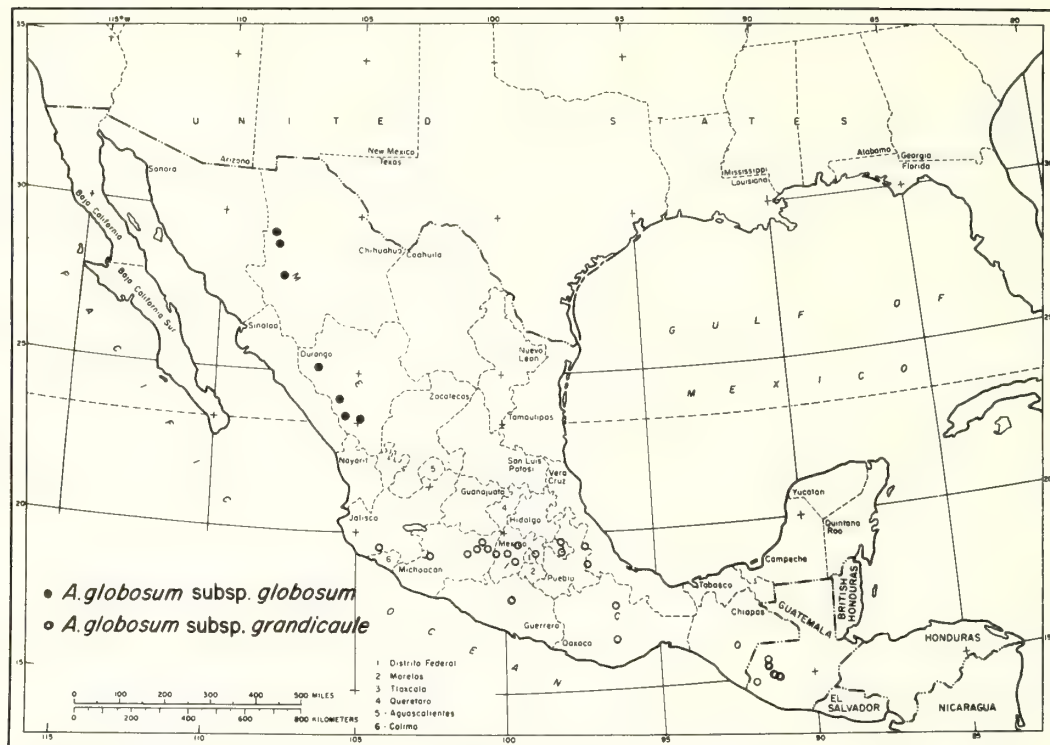


Figure 1.--Distribution of the two subspecies of *Arceuthobium globosum* in Mexico and Guatemala.

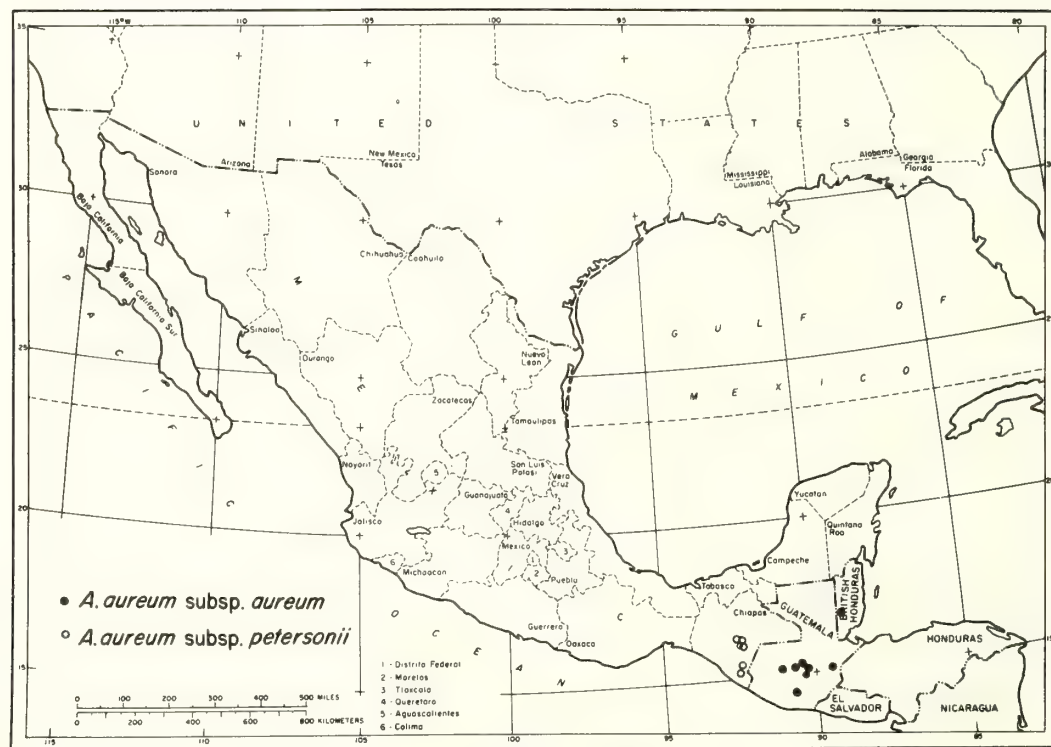


Figure 2.--Distribution of the two subspecies of *Arceuthobium aureum* in Mexico, Guatemala, and Belize.

3. ARCEUTHOBIUM AUREUM subsp. PETERSONII. This local taxon is known only in Chiapas, Mexico, where it parasitizes at least 6 species of pines (fig. 1). Plants of this taxon are nearly twice the size of subsp. aureum and it sometimes forms witches' brooms.

4. ARCEUTHOBIUM PENDENS. This species parasitizes pinyons and is presently known from only two locations in Mexico: San Luis Potosí on Pinus discolor, and in Veracruz on P. cembroides subsp. orizabensis (Hawksworth and Wiens 1980). It is distinguished by its tall, slender shoots (up to 22 cm) and formation of systemic witches' brooms by the staminate (but apparently not the pistillate) plants.

5. ARCEUTHOBIUM CUBENSE. The recent report of this species, a parasite of the endemic Podocarpus ekmanii Urban in eastern Cuba, is a surprise (Leiva and Bisse 1983). This is the first report of Arceuthobium on hosts outside the Pinaceae or Cupressaceae.⁴ The species was formerly classed as Dendrophthora cupressoides, a widespread Caribbean species on several hosts including Juniperus (Kuijt 1961). We have seen no specimens of A. cubense so we are unable to comment on its validity; however, the report is so exceptional that verification is needed.

Old World

In our 1972 monograph we mentioned that the vast geographic range and widely disjunct populations in A. oxycedri might necessitate recognition of additional species. This is the case, and we now recognize 3 species formerly included under "A. oxycedri": A. oxycedri sensu stricto on several species of junipers from the Mediterranean area through the Middle East to China; A. juniperi-procerae on Juniperus procera in Kenya and Ethiopia, and A. azoricum on J. brevifolia in the Azores (Hawksworth and Wiens 1976).

6. ARCEUTHOBIUM AZORICUM. This species is restricted to the endemic Juniperus brevifolia on several islands of the Azores (Hawksworth and Wiens 1976). It is unique because of its distinct habit, especially its thick shoots--nearly 1 cm in diameter, which is 2 to 3 times larger than A. oxycedri or A. juniperi-procerae, and the very high proportion of 4-merous flowers.

7. ARCEUTHOBIUM JUNIPERI-PROCERAE. This species, a parasite on Juniperus procera, was described by Chiovenda (1911). Our studies in Ethiopia and Kenya show that it differs from A. oxycedri sensu stricto in several respects: occurrence of whorled branching, phenology, shoot color, and shoot glaucousness (Hawksworth and Wiens 1976). This species is the only member of the genus that occurs south of the equator. Possibly this species occurs in Juniperus procera north of the Red Sea in Yemen.

⁴Arceuthobium dacrydi, described on Podocarpus from Java, has since been shown to be a Korthalsella (Hawksworth and Wiens 1972).

8. ARCEUTHOBIUM TIBETENSE. This species was recently described from Xizang (Tibet) where it is a local parasite of Abies georgei (Kiu and Ren 1982, Kiu 1984).

9. ARCEUTHOBIUM PINI var. SICHUANENSE. This parasite of Picea has a broad distribution in southwestern China (Sichuan and Tibet) (Kiu 1984). A distribution map for it is given by Kiu and Ren (1982). Variety sichuanense is much smaller than A. pini var. pini on Pinus.

STATUS OF PREVIOUSLY KNOWN TAXA

Here we summarize the current taxonomic status and significant extensions in geographic or host ranges since publication of our 1972 monograph (Hawksworth and Wiens 1972).

New World

1. ARCEUTHOBIUM ABIETINUM f. sp. CONCOLORIS. This mistletoe parasitizes Abies concolor and A. grandis, primarily in California and Oregon, with isolated locations in Washington, Nevada, Utah, and Arizona. No new hosts have been reported for this mistletoe. Several new localities for it have been reported (fig. 3), especially in Oregon, Utah, Nevada, and in southern Arizona (Mathiasen 1976, Mathiasen and Jones 1983). The latter are of particular interest as they represent range extensions of about 500 km.

2. ARCEUTHOBIUM ABIETINUM f. sp. MAGNIFICA. This taxon parasitizes Abies magnifica in California and this host and A. procerae in southern Oregon. A few new localities have been reported but all are within the limits of the range of the taxon as known in 1972.

3. ARCEUTHOBIUM ABIETIS-RELIGIOSAE. This parasite of Abies is common in central Mexico. Since 1972, the mistletoe has been reported in four additional states: Michoacán, Puebla, Tamaulipas, and Tlaxcala (Hawksworth and Wiens 1977).

4. ARCEUTHOBIUM AMERICANUM. This is one of the most widely distributed dwarf mistletoes in North America, ranging from California and Colorado to British Columbia on Pinus contorta, and eastward on P. banksiana to Ontario. Pseudotsuga menziesii is a rare host in Alberta (Muir 1973); it was previously reported as rare on this tree in Utah (Hawksworth and Wiens 1972). The parasite has been found on P. contorta ssp. contorta in a few locations in coastal British Columbia (Smith and Wass 1979), but we have not been able to confirm the early report of A. americanum on this subspecies in the Oregon Mountain area of southwestern Oregon. Several new locations for A. americanum have been reported (fig. 4). The mistletoe is now known from most of the isolated populations of Pinus contorta in central Montana (all except the Highwood and Big Snowy mountains--Dooling and Eder 1981). A detailed distribution map for A. americanum in British Columbia has been published by Baranyay and Bauman (1972). No new locations have been found between the eastern limits of the mistletoe in southeastern Manitoba and the disjunct locality near Lac Seul in Ontario.

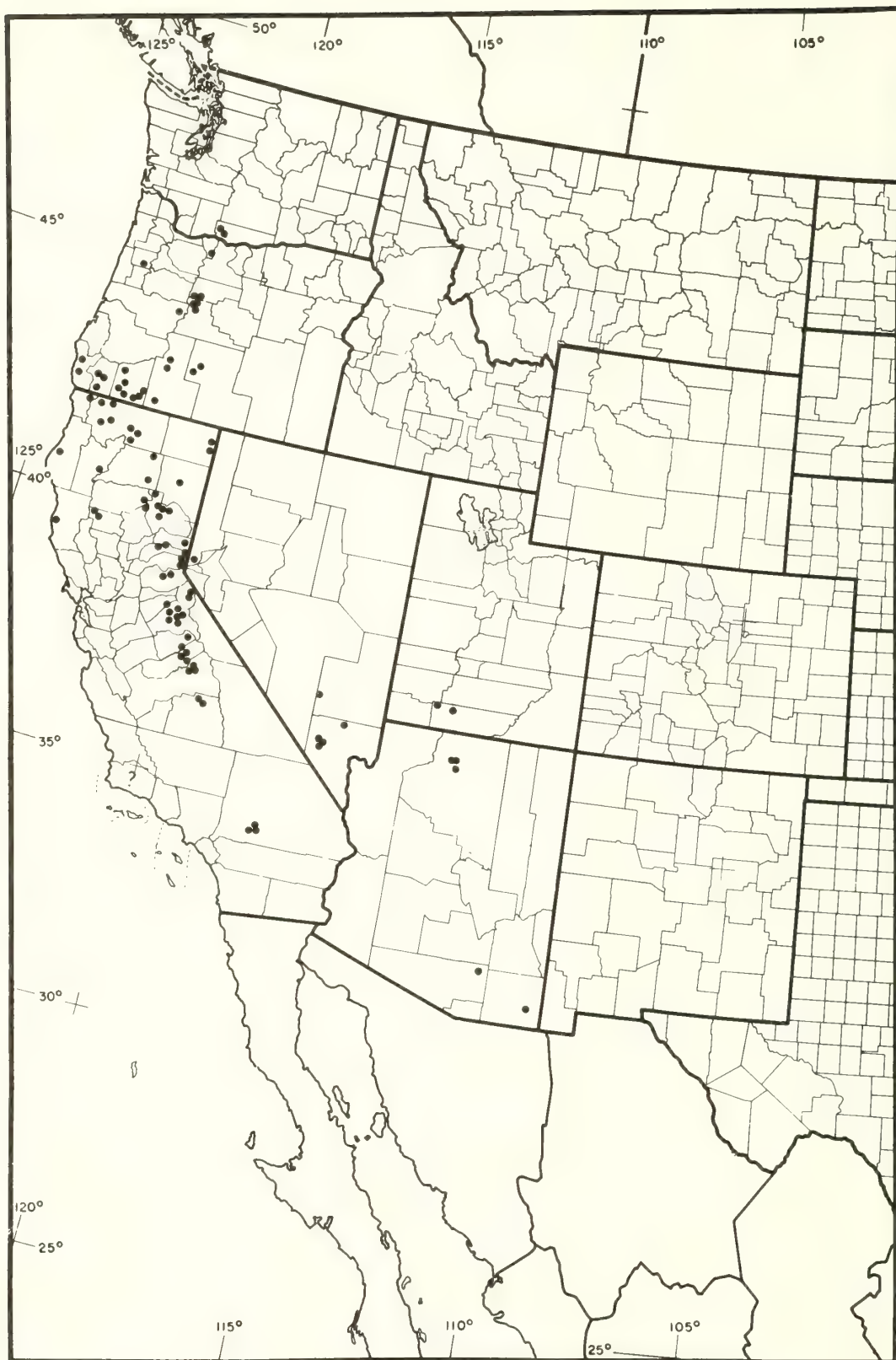


Figure 3.--Distribution of *Arceuthobium abietinum* f. sp. *concoloris*. Smith's (1976) reports on Big Pine Mountain and Reyes Peak near Santa Barbara have not been confirmed.

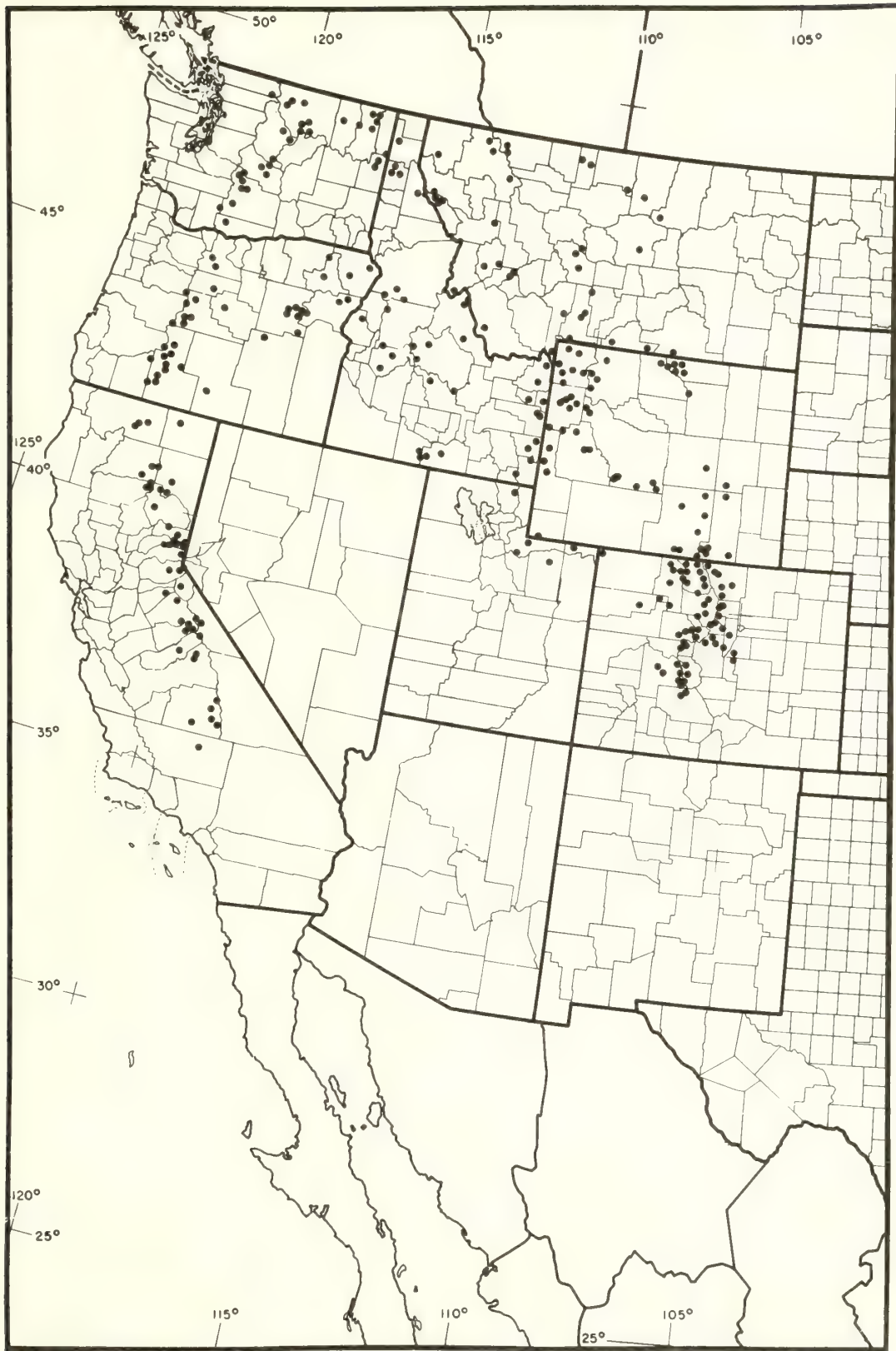


Figure 4.--Distribution of *Arceuthobium americanum* in the western United States.

Due to fire and logging, this local population in Ontario may be extinct (Myren and Gross 1977).

5. ARCEUTHOBIUM APACHECUM. No major extensions in the range of this local parasite of Pinus strobiformis in Arizona, New Mexico, and Coahuila, Mexico have been found (Mathiasen 1979). However, in inoculation tests, Pinus flexilis was found to be susceptible to A. apachecum (Mathiasen 1978). The populations that we classified as A. blumeri in the Santa Rita Mountains in southern Arizona have since been found to be A. apachecum (Mathiasen 1982).

6. ARCEUTHOBIUM BICARINATUM. No new information on this parasite of Pinus occidentalis in Hispaniola has been reported.

7. ARCEUTHOBIUM BLUMERI. This is a local parasite of Pinus strobiformis in northern Mexico and in a single locality in the United States (Huachuca Mountains, Arizona). Mathiasen (1979), 1982) reports an additional native host: P. ayacahuite var. brachyptera in Durango, Mexico, and also found, by greenhouse inoculations, that P. flexilis is susceptible (Mathiasen 1978). The parasite is also reported for the first time in Sonora (Ajo Mountains--Mathiasen 1979). The species has been found in a few new locations in Mexico, but mostly near previously known localities (Cibrian T. et al. 1980, Hawksworth and Cibrian T. 1984).

8. ARCEUTHOBIUM CALIFORNICUM. This parasite is common on Pinus lambertiana and P. monticola in California and Oregon. The only major range extension is a report on Big Pine Mountain near Santa Barbara (Smith 1976), but no specimens from that area have been seen.

9. ARCEUTHOBIUM CAMPYLOPODUM. This widespread parasite, mainly of Pinus ponderosa and P. jeffreyi, is found from northern Washington and western Idaho to Baja California, Mexico. The only new host reported is the introduced Pinus halepensis, in the Angeles National Forest, California (collected by R. F. Scharpf in 1972, specimen at FPF). A few new locations have been reported, but most are within the geographic range known in 1972. An exception is a collection in the Wallamette Valley of Oregon, about 10 miles south of Corvallis. A collection was made in 1942 by L. F. Roth, and we recently found the mistletoe in the same area. However, ponderosa pine has been severely logged in this area and the mistletoe population is surviving only on a few old-growth trees. This population will probably soon become extinct.

10. ARCEUTHOBIUM CYANOCARPUM. This is a widespread, but local, parasite primarily of Pinus flexilis (and to a lesser extent of P. aristata) in the western United States (fig. 5). Two locations previously thought to be A. cyanocarpum are now known to be other taxa, (1) the San Francisco Peaks population in Arizona is A. microcarpum (Mathiasen and Hawksworth 1980), and (2) the Hawley Lake, Sierra County, California collection is A. tsugense. Several new

locations of A. cyanocarpum have been found (fig. 3) including the first verified report in Oregon (Three Creek Lakes, Deschutes County--Knutson and Tinnin 1981); the Panamint Mountains, California (Johnson 1976), and in southern Colorado. A unique population of A. cyanocarpum was found near Boulder, Colorado, in a pure Pinus ponderosa stand. The closest known infection on its usual host, P. flexilis, is at least 5 miles away and 2000 feet higher (Hawksworth et al. 1975). Tsuga mertensiana is a new host for A. cyanocarpum (Oregon, Knutson and Tinnin 1981). "Pinus aristata," as formerly understood, is now known to comprise two distinct species, Pinus longaeva D. K. Bailey in the Great Basin (California, Utah, and Nevada), and P. aristata sensu stricto in the Rocky Mountains (Colorado, New Mexico, and Arizona (Bailey 1970). Pinus longaeva is frequently parasitized by A. cyanocarpum in Nevada and Utah; the mistletoe is known only on P. aristata in one locality in southern Colorado.

11. ARCEUTHOBIUM DIVARICATUM. This widespread dwarf mistletoe of the southwestern United States and northern Baja California, Mexico, is still known only on the pinyons. By far its most common hosts are Pinus edulis and P. monophylla. It was previously known also on P. cembroides only in the Davis Mountains of West Texas, and P. quadrifolia in Baja California, but it has since been found on two additional taxa: Pinus discolor in southern New Mexico, and P. edulis var. fallax in Arizona and Utah. Several new locations of the parasite have been found since 1972, but most are within its previously known limits (fig. 6).

12. ARCEUTHOBIUM DOUGLASII. No major range extensions of this widespread parasite of Pseudotsuga menziesii have been reported. See Baranyay and Bauman (1972) for its distribution in British Columbia. New locations found are: the first for coastal British Columbia (near Chilliwack (Van Sickle and Fiddick 1982), and in northwestern Durango, Mexico (Cibrian T. et al. 1980). In 1981, we examined most of the Pseudotsuga stands in Chihuahua but did not discover the parasite there (Hawksworth and Cibrian T. 1984). Cibrian T. et al. (1980) report A. douglasii on Pseudotsuga flahaultii in Durango, but we question whether this tree is distinct from P. menziesii var. glauca. Palmer et al. (1983) report A. douglasii in the Sierra Nevadas in Placer County, about 75 miles south of its previously known southern limits in California, but this has not been confirmed. Dooling and Eder (1981) show the known distribution of A. douglasii in Montana.

13. ARCEUTHOBIUM GILLII. This parasite, primarily of Pinus leiophylla var. chihuahuana, is found in northern Mexico and the southwestern United States (fig. 7). New locations for the parasite include: New Mexico (Animas Mountains, Hawksworth and Weiss 1975), Sonora (Ajo Mountains, Mathiasen 1979b), and northern Sinaloa. Pinus cooperi (Chihuahua) is a new host (Hawksworth and Cibrian T. 1984).

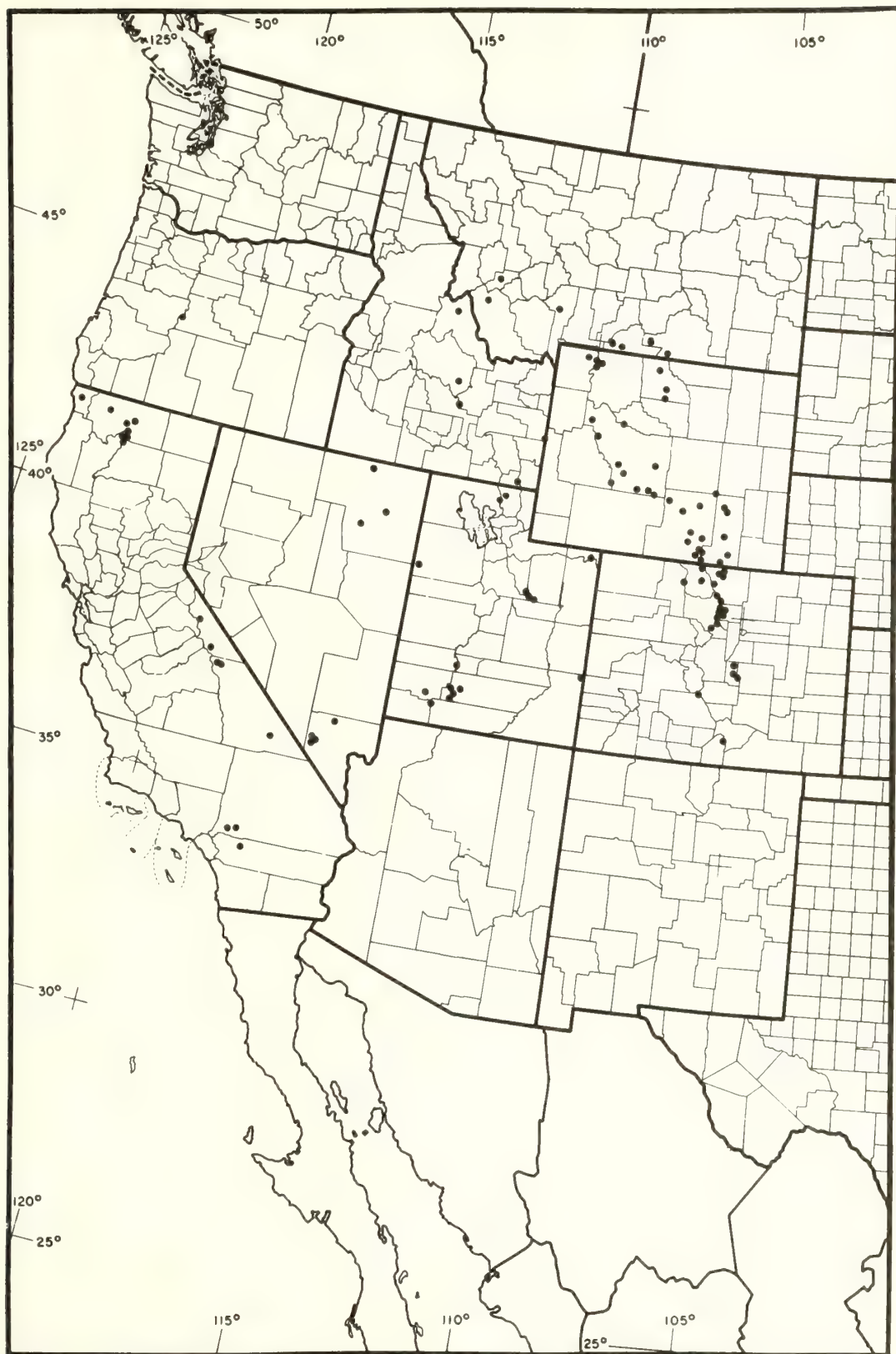


Figure 5.--Distribution of *Arceuthobium cyanocarpum*.

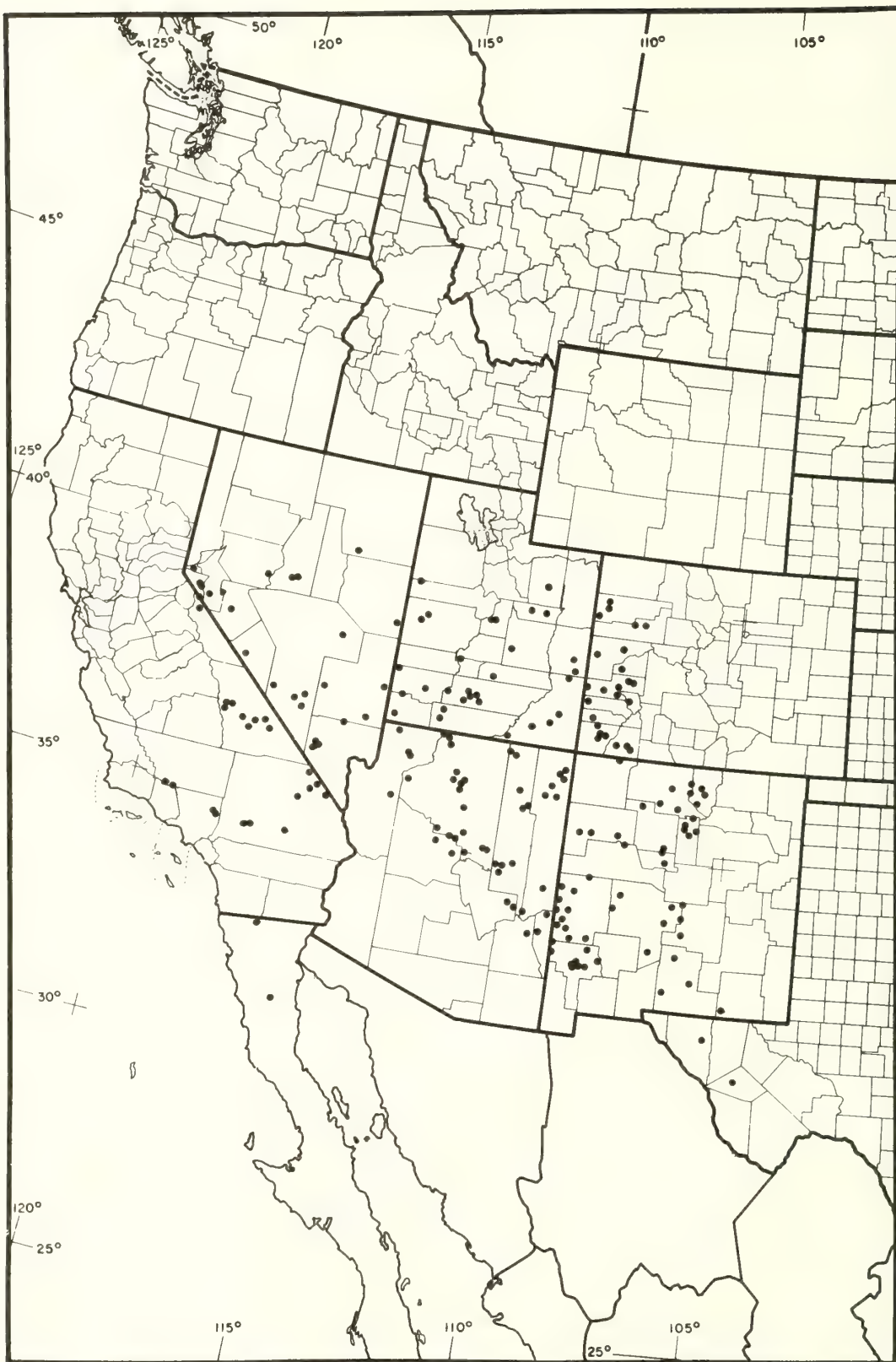


Figure 6.--Distribution of *Arceuthobium divaricatum* in the United States and Mexico.

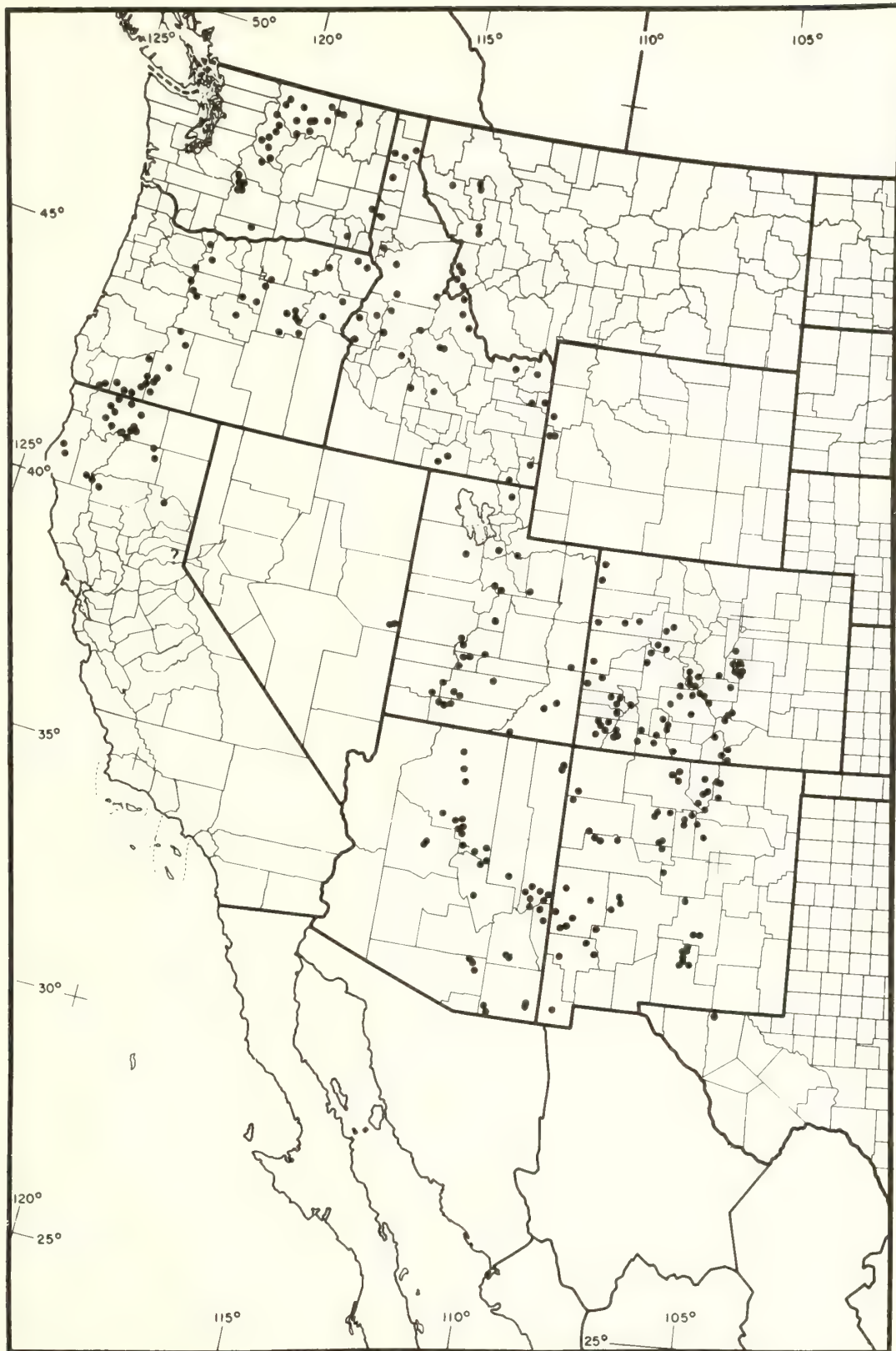


Figure 7.--Distribution of *Arceuthobium douglasii* in the western United States. The report by Palmer et al. (1983) in Placer County, California has not been confirmed.

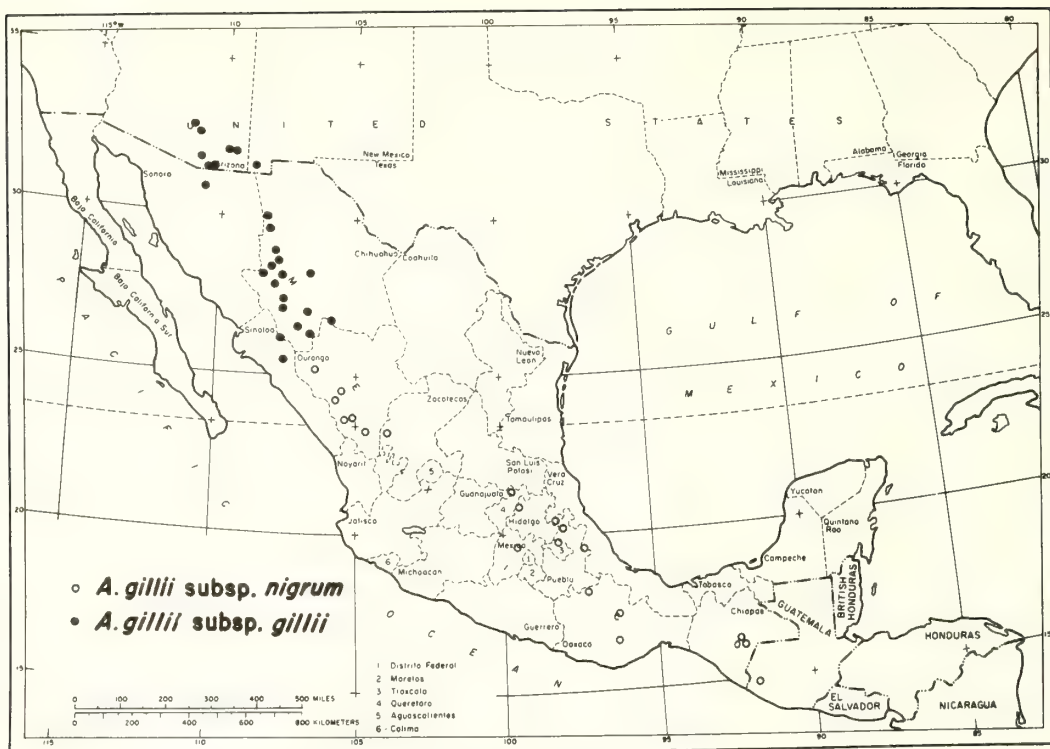


Figure 8.--Distribution of the two subspecies of Arceuthobium gillii in Mexico and the southwestern United States.

14. ARCEUTHOBIUM GILLII subsp. NIGRUM. This parasite of Mexican pines (mainly P. leiophylla var. leiophylla) has been found in several new locations in the States of Queretaro, Zacatecas, Mexico, Puebla, Oaxaca, and Chiapas (fig. 8). New hosts include Pinus oaxacana (Chiapas), P. lawsonii (Oaxaca), P. patula (Chiapas and Puebla), and P. herrerae (Oaxaca), P. patula (Chiapas and Puebla), and P. herrerae (Oaxaca) (Hawksworth and Wiens 1977). We have reports of the taxon in the San Marcos area of Guatemala, but we have seen no collections from that country.

15. ARCEUTHOBIUM GLOBOSUM. This parasite of pines in northern Mexico was reported from Chihuahua and Durango, and has since been found in Sonora (fig. 1). As noted by Hawksworth and Wiens (1977), selection of the type of A. globosum was unfortunate because that population consists of a small plant presently known only from the area around El Salto, Durango on Pinus cooperi. The more common phase of the species is much larger and occurs on other pines (P. arizonica, P. durangensis, and P. engelmannii). Although there are some differences between the small plant composing a single geographically restricted type population and the widespread, larger, rounded form, these do not, at present, appear to be sufficient to warrant taxonomic recognition.

16. ARCEUTHOBIUM GUATEMALENSE. This parasite of

Pinus ayacahuite was described from Guatemala but has since been found in Chiapas and Oaxaca in southern Mexico (Hawksworth and Wiens 1977).

17. ARCEUTHOBIUM HONDURENSE. No new information on this parasite of pines in Honduras has been reported, but it possibly occurs in the Monte Cristo area in northeastern El Salvador (Hawksworth 1982). It is probably the rarest of all the dwarf mistletoes.

18. ARCEUTHOBIUM LARICIS. This is a widespread parasite of Larix occidentalis in Montana, Idaho, Oregon, Washington, and British Columbia. Smith et al. (1972) reported the first known instances in British Columbia of this species on Abies grandis and Pinus ponderosa, which were also rare hosts of it in the U.S. Smith and Wass (1972) showed by inoculations that Abies amabilis is rarely infected by A. laricis. Distribution maps for A. laricis have been published for British Columbia (Baranyay and Bauman 1972), and Montana (Dooling and Eder 1981). A few new localities have been reported in the United States but all are within the previously known range.

19. ARCEUTHOBIUM MICROCARPUM. This species has a highly local distribution, primarily on Picea in Arizona and New Mexico. In the San Francisco Peaks, Arizona, A. microcarpum is common and damaging on Pinus aristata (Mathiasen and Hawksworth 1980). We tentatively classed this population as A. cyanocarpum (Hawksworth and Wiens

1972). Mathiasen (1978) showed in greenhouse tests that P. flexilis is susceptible to A. microcarpum. A major range extension of A. microcarpum is the recent discovery of an isolated population in the Sacramento Mountains in southern New Mexico, some 270 km east of its previously known limits in the Mogollon Mountains (Mathiasen and Jones 1983).

20. ARCEUTHOBIUM OCCIDENTALE. This species is confined to California where it is found on a number of hard pines. Its principal hosts are Pinus sabinana, P. radiata, and P. muricata; it sometimes parasitizes P. coulteri, P. attenuata, and P. contorta subsp. bolanderi. Contrary to reports in our 1972 monograph, the species does infect P. ponderosa, at least in the Santa Lucia Mountains. Possibly A. occidentale may also parasitize Pinus jeffreyi on the San Benito Mountains where a few infected Jeffrey pines were observed in infected P. sabiniana-P. coulteri stands (Griffin 1975). A few new locations for A. occidentale have been reported, but all are within the general range previously reported. The taxonomic status of this species and its relation to A. campylopodum are discussed in the "Taxonomic Problems" section of this paper.

21. ARCEUTHOBIUM PUSILLUM. No major changes in the hosts or geographic distribution of this species have been reported. However, our observations in New Hampshire suggest that Picea rubens should be considered a principal host because A. pusillum is widespread in pure stands of this tree (Hawksworth and Shigo 1980). A. pusillum was also found in a Pinus banksiana stand near Isabella, Minnesota (Baker et al. 1978). Coulombe (1973) reported Abies balsamea as a new host for A. pusillum in St. Jean, Quebec. The tree was transplanted from a bog in the Farnham region and probably became infected there. Distribution maps of A. pusillum have been published for Quebec (Lavallee 1973), Ontario (Myren and Gross 1977), and Newfoundland (Singh 1982). A survey in the Lower Peninsula of Michigan showed the mistletoe to be quite local (Mathiasen 1979).

22. ARCEUTHOBIUM RUBRUM. This rare Mexican parasite of pines was previously known only in local areas in the Sierra Madre Occidental of Durango and Sinaloa. Since then, a disjunct population nearly 1200 km southeast from the Sierra Madre populations was found in southern Oaxaca by R. S. Peterson (Hawksworth and Wiens 1977). In Oaxaca, the principal hosts are Pinus lawsonii, P. michoacana, and P. pseudostrobus; P. oaxacana is occasionally parasitized. In Durango, the mistletoe parasitizes P. cooperi, P. durangensis, P. engelmanni, P. teocote, and P. herrerae, but none of these pines occur at the Oaxacan site. The status of the southern population deserves further study.

23. ARCEUTHOBIUM STRICTUM. This very distinctive, but rare, species on pines is still known only from a few locations in Durango, Mexico.

Player (1979) investigated its pollination ecology.

24. ARCEUTHOBIUM TSUGENSE. This common parasite of Tsuga heterophylla ranges from near Haines, Alaska to northern California. A distribution map for British Columbia was published by Baranyay and Bauman (1972). It is rare on Tsuga mertensiana in Alaska and British Columbia (Shaw 1982, Van Sickle and Fiddick 1982), but this is its most frequent host in the mountains of Oregon and California. Inoculation studies with Pseudotsuga menziesii indicated that the species could be rarely infected by A. tsugense (Smith and Wass 1972), and also P. menziesii has recently been reported to be a rare, natural host in British Columbia (Hunt and Smith 1978). The status of the race of this mistletoe on shore pine (Pinus contorta subsp. contorta) is still in question. Extensive populations of A. tsugense occur on this pine from the San Juan Islands, Washington, along the eastern shore of Vancouver Island, and coastal British Columbia (Smith 1974, Smith and Wass 1976, Wass 1976).

25. ARCEUTHOBIUM VAGINATUM subsp. VAGINATUM. This large, widespread Mexican species attacks at least 12 species of pines, and ranges from west-central Chihuahua to northern Oaxaca, and north in the Sierra Madre Oriental to southern Coahuila (fig. 9). It has been found for the first time in Sinaloa.

26. ARCEUTHOBIUM VAGINATUM subsp. CRYPTOPODUM. This common and damaging parasite, mainly of Pinus ponderosa var. scopulorum, ranges from northern Colorado and central Utah to Chihuahua and Coahuila, Mexico (fig. 9). Several new locations for the parasite have been found but most of them, except in Coahuila, are within the previously known range of the taxon. New hosts for this subspecies are Pinus cooperi and P. durangensis in Chihuahua (Hawksworth and Cibrian T. 1984).

27. ARCEUTHOBIUM VAGINATUM subsp. DURANGENSE. This local taxon is known mainly from along the Durango-Mazatlan highway in western Durango and adjacent parts of Sinaloa (Hawksworth and Wiens 1977) (fig. 9). It was recently collected near Cosala, Sinaloa, about 150 km to the north of its previously known limits (collected by R. L. Mathiasen, specimen at FPF).

28. ARCEUTHOBIUM VERTICILLIFLORUM. This primitive Mexican species is the most distinctive dwarf mistletoe. It is characterized by its large fruits (over 1 cm long) and its verticillate staminate flowers. It was previously known only from the vicinity of El Salto, Durango, but a second population was recently discovered at El Huacal, Durango, about 200 km to the north (Cibrian T., et al. 1980).

Old World

29. ARCEUTHOBIUM CHINENSE. This small species parasitizes Keteleeria in southwestern China (Yunnan and Sichuan provinces). The occurrence



Figure 9.--Distribution of the three subspecies of *Arceuthobium vaginatum* in the United States and Mexico. Only the southern United States collections of subsp. *cryptopodum* are shown.

of 4-parted staminate flowers distinguishes this species from other Chinese taxa, which are primarily 3-parted. The only known distribution map for *A. chinense* was recently published by Kiu and Ren (1982). Kiu (these proceedings) notes that reports of this species on *Abies* are in error and probably based on misidentification.

30. *ARCEUTHOBIUM MINUTISSIMUM*. This species is essentially restricted to *Pinus wallichiana*, a high altitude pine of the Himalayas. It occurs in northern Tibet.⁵ This very small species (with shoots only about 5 mm high) was thought to be exclusively parasitic on *Pinus wallichiana*. However, *Pinus gerardiana* was recently found to be a rare host of this mistletoe in areas where this tree occurs in mixed stands with *Pinus wallichiana* in Pakistan (Zakauallah and Badshaw 1984). Rechinger (1976) reports it on *Cedrus deodara* in Pakistan, but this record has not been confirmed. The recent report of *A. minutissimum* at low elevations in southern India on an angiosperm (Gaur 1981) is in error and was based on a fungus that superficially resembles the dwarf mistletoe.

31. *ARCEUTHOBIUM PINI*. This parasite of pines in southwestern China was previously known from Yunnan and Sichuan provinces. It was recently found in Tibet by Kiu and Ren (1982), who present the only known distribution map for this species.

32. *ARCEUTHOBIUM OXYCEDRI*. This parasite of junipers has a vast range of over 9,000 km from

Spain throughout the Middle East, and to Pakistan, India, and Tibet (Hawksworth and Wiens 1976, Kiu and Ren 1982). Hawksworth and Wiens (1976) list it on 10 species of junipers, and Lararev and Girgorov (1980) record it on 3 additional species in the Crimea, USSR. They also found it on introduced *Juniperus thujifera*. Kiu (these proceedings) lists it on two new hosts: *Sabina* (*Juniperus*) *wallichiana* and *S. tibetense* in Tibet.

SYNOPSIS OF THE GENUS

As currently recognized, the genus *Arceuthobium* comprises 41 taxa, 33 in the New World, and 8 in the Old (Table 1). The countries with the greatest increase since 1972 are China (2 to 6 taxa), Mexico (16 to 19), and Guatemala (2 to 5). Since 1972, *Arceuthobium* has been first reported in El Salvador and Cuba (assuming that *A. cubense* is, in fact, a dwarf mistletoe).

TAXONOMIC PROBLEMS IN *ARCEUTHOBIUM*

Although we feel that we have the "big picture" of the genus *Arceuthobium* in the world there are a number of taxonomic questions that remain to be resolved.

1. For some time, it has been recognized that the populations of *Arceuthobium tsugense* on shore pine (*Pinus contorta* subsp. *contorta*) may be distinct from those on *Tsuga heterophylla*. Populations on *Pinus* rarely infect *Tsuga* and vice versa (Smith and Wass 1976). Taxonomic studies of the two races, or pathotypes, are underway. Perhaps they should be treated as *forma speciales* (as we have done for *A. abietinum* on

⁵Personal communication, Chen Mo-me, forest pathologist, Academy of Forestry, Beijing, 1982.

Abies concolor and A. magnifica), or as subspecies, if consistent morphological differences can be found. The populations on Tsuga mertensiana and white pines in southern Oregon and California may also be distinct.

2. The Arceuthobium campylopodum-A. occidentale alliance is more complex than we originally thought. For example, in the monograph we listed Pinus ponderosa, a primary host of A. campylopodum, as immune to A. occidentale. This is not the case, since A. occidentale is locally common on P. ponderosa as well as P. coulteri in the Santa Lucia Mountains in California. Branching patterns of A. occidentale and A. campylopodum are distinct (Mark and Hawksworth 1982). A series of cross-inoculation studies of A. occidentale and A. campylopodum conducted by W. Mark and R. Scharpf on several pines in various parts of California should shed light on the taxonomic relationships of these two economically important taxa.

3. The status of several Mexican taxa, particularly the subspecies of A. globosum, A. gillii, and A. vaginatum, and the two populations of A. rubrum, should be re-evaluated. Some of these may warrant specific status, as the differences between them are at least as great as between several recognized species in section Campylopoda.

4. The status of the recently described A. cubense in Cuba should be confirmed. If this turns out to be a valid Arceuthobium on a member of the Podocarpaceae, we may have to re-evaluate our speculation that the genus arose in eastern Asia as a parasite of pines.

5. Now that eight members of the genus are known from the Old World, it would be worthwhile to attempt to develop supra-specific categories for them.

6. Incorporation of data from new taxonomic approaches, such as isozyme electrophoresis, should be useful in helping understand the taxonomy and evolutionary relationships of the dwarf mistletoes (see papers by Nickrent et al. and Linhart, these proceedings).

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Arceuthobium and its Hosts in Southwestern China¹

Kiu Hua-shing²

Abstract.--Arceuthobium is represented in Southwestern China by five taxa, two of which were recently described: A. tibetense H. S. Kiu et W. Ren (1982) on Abies in Xizang, and A. pini var. sichuanense H. S. Kiu (1984) on Picea in Xizang and Sichuan. The other three known taxa are A. chinense on Keteleeria in Sichuan and Yunnan; A. pini on Pinus in Xizang, Sichuan, and Yunnan; and A. oxycedri on Sabina in Xizang. Reports of A. chinense on Abies are questioned as the mistletoe is not known within the elevational range of Abies.

INTRODUCTION

The Chinese name of Arceuthobium M. Bieb. is You-shan-ji-sheng Shu. It is widely distributed in Southwestern China and is represented by 5 taxa: 4 are found in Xizang (Tibet) Autonomous Region, 3 in Sichuan Province, and 2 in Yunnan Province (Table 1). Their known elevational range is from 1,500 to 4,100 meters.

Table 1.--Distribution of Arceuthobium in Southwestern China

Taxon	Xizang	Sichuan	Yunnan
<u>A. chinense</u>	----	X	X
<u>A. pini</u>	X	X	X
<u>A. pini</u> var. <u>sichuanense</u>	X	X	----
<u>A. tibetense</u>	X	----	----
<u>A. oxycedri</u>	X	----	----
Number of taxa	4	3	2

Note: (----) indicates not known in the Province (Region).

The paper is based on examining specimens collected by the Chinese botanists through many expeditions during the last fifty years, and those of my field work in recent years.

Biologic characteristics presented for each of the 5 taxa include: diagnosis, hosts; (Table 2), and others.

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Table 2.--Hosts of Chinese dwarf mistletoes

<u>Arceuthobium</u>	Principal host	Secondary host
<u>A. chinense</u>	<u>Keteleeria evelyniana</u>	
<u>A. pini</u>	<u>Pinus densata</u>	<u>Pinus yunnanensis</u>
<u>A. pini</u> var. <u>sichuanense</u>	<u>Picea likiangensis</u> var. <u>balfouriana</u>	
<u>A. tibetense</u>	<u>Abies georgii</u>	
<u>A. oxycedri</u>	<u>Sabina wallichiana</u>	
	<u>Sabina tibetica</u>	

1. Arceuthobium chinense Lecomte (1915). (Keteleeria dwarf mistletoe).

Plants 2-8 (10-12) cm. high, yellowish-green or green; branches opposite, rarely 3-4 (-6) verticillate; basal diameter of dominant shoots 1-2 mm. Flowers axillary or terminal; male flower ca. 2 mm. in diameter, perianth segments 4, lobes subtriangular, ca. 1.5 mm. long; female flower greenish, 1 mm. long. Mature fruit ovoid, 4-6 mm. long and 3-4 mm. wide, proximal portion yellowish-green or glaucous. Flowering period: July to October. A. chinense induces systemic witches' brooms on Keteleeria evelyniana Mast., which is its only actual host. In central and northwestern Yunnan and southwestern Sichuan at elevational range of 1,500 to 2,700 m.

According to M. H. Lecomte's (1915) original description: this dwarf mistletoe is parasitic on the Abies and the type specimen of A. chinense (Delavay s.n.) (n.v.) was collected at Ta-pin-tze in Yunnan. But this locality is only 2,470 m. above sea level; no species of Abies has been found in such low altitude. So, its possible that M. H. Lecomte misidentified the host plant.

2. Arceuthobium pini Hawsworth et Wiens (1970). (Alpine pine dwarf mistletoe)

Plants 5-15 (-20) cm. high, greenish-yellow or greenish; branches opposite, rarely 3-4 verticillate; basal diameter of dominant shoots 1.5-2.5 mm. Male flowers 1 or 2 terminal on short branches, 2-2.5 mm. in diameter, perianth segments 3, rarely 4, lobes 1-1.5 mm. long. Female flowers terminal or axillary, ca. 1 mm. long. Mature fruit ellipsoid, 3-4 mm. long and 2-2.5 mm. wide, proximal portion greenish-yellow. Flowering period: April to June. It is known to be parasitic on Pinus densata Mast. and P. yunnanensis Fr.; these infected hosts did not form witches' brooms. In eastern Xizang, northwestern Yunnan, and southeastern Sichuan at elevational range of 2,700-3,500 (-4,000) m.

2a. Arceuthobium pini Hawsworth et Wiens var. sichuanense H. S. Kiu in Acta Phytotax. Sinica 22(3): 1984.

Plants 2-6 cm. high, greenish-yellow; basal diameter of dominant shoots 1-1.5 mm. Flowers axillary or terminal on short branches; male flower 1.5-2 mm. in diameter, perianth segments 3. Mature fruit ellipsoid, 3-4 mm. long and 1.5-2 mm. wide. Flowering period: June to July. Parasitic on Picea likiangensis (Fr.) Pritz. var. balfouriana (Rehd. et Wils.) Hallier ex Slavin; host induced to systemic witches' brooms. In eastern Xizang and western Sichuan. Known elevational range is 3,800 to 4,100 m.

Specimens examined: Sichuan: Dawu, in 1974, Y. T. Wu et B. C. Gao 111629, ♂ (type CDBI). Xizang: Biru, in 1976, T. T. Dao 11287, ♀ (KUN).

3. Arceuthobium tibetense H. S. Kiu et W. Ren (1982).

Plants 0.5-2.2 cm. high, yellowish-green, branches opposite; basal diameter of dominant shoots ca. 1.5 mm. Flowers terminal or axillary; male flower 2 mm. in diameter, perianth segments 3, rarely 4, lobes subtriangular, ca. 1.2 mm. long. Fruit ellipsoid, ca. 2 mm. long, proximal portion glaucous. Flowering period: May to June. Parasitic on Abies georgei Orr and induces witches' brooms. In eastern Xizang at an elevation ca. 3,400 m. in fir forest.

Specimens examined: Xizang: Mainling, in 1981, K. Z. Chao 14, ♂ (SCBI), ibidem, K. Z. Chao 14 A, ♀ (SCBI).

4. Arceuthobium oxycedri (DC.) M. Bieb. (1819).

Plants 5-16 cm. high, greenish-yellow; branches opposite, rarely 4-6 verticillate; basal diameter of shoots 1.5-3 (-4) mm. Male flowers solitary or 2-3 terminal on short branches, ca. 2 mm. in diameter, perianth segments 3, sometimes 4. Female flowers terminal or axillary. Fruit ellipsoid, ca. 3 mm. long.

Flowering period: August to September. Parasitic on Sabina wallichiana (Hook. f. et Thoms.) Kom. and S. tibetica Kom. In eastern Xizang at elevational range of 3,000 to 3,500 m.

Specimens examined: Xizang: Riwoke, in 1952, P. C. Tsoong 5319 (PE); Bomi, in 1965, T. S. Ying et al. 1984 (PE). These specimens might be a geographic variation of the widespread species A. oxycedri.

Key to the dwarf mistletoes in southwestern China (Kiu and Ren 1982).

1. Staminate sepals 4; basal diameter of dominant shoots 1-2 mm.; plants 2-8 (12) cm. high; side branches frequently less than 1 cm. long; parasitic on Keteleeria (Yunnan, Sichuan).

. A. chinense Lecomte

1. Staminate sepals 3, rarely 4.

2. Parasites of Pinaceae

3. Plants 5-20 cm. high; basal diameter of dominant shoots 1.5-2.5 mm.; side branches longer than 1 cm., staminate flowers 2-2.5 mm. wide; sepals 3 rarely 4; parasitic on Pinus (Yunnan, Sichuan, Xizang)
. A. pini Hawsworth et Wiens

3. Plants frequently less than 5 cm. high, basal diameter of dominant shoots 1-1.5 mm. wide.

4. Parasitic on Picea; plants 2-6 cm. high; side branches about 1 cm. long, staminate flowers 1.5-2 mm. wide; sepals 3 (Sichuan, Xizang).
. A. pini var. sichuanense H. S. Kiu

4. Parasitic on Abies; plants 0.5-1.7 (2.2) cm. high; side branches 3-6 mm. long; staminate flowers 2 mm. wide; sepals 3, rarely 4 (Xizang).
. A. tibetense H. Kiu et W. Ren

2. Parasites of Cupressaceae (Sabina), plants 5-16 cm. high; staminate flowers 2 mm. diameter; sepals 3, rarely 4 (Xizang, A. oxycedri (DC.) M. Bieb.

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Biosystematic and Evolutionary Relationships among Selected Taxa of *Arceuthobium*¹

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Abstract: Genetic relationships within 19 taxa of New World *Arceuthobium* were examined using starch gel electrophoresis of seed endosperm. Allelic frequency data for 11 polymorphic loci from forty populations of the above taxa were compared using unweighted pair group cluster analysis and Nei's genetic identity. *Arceuthobium americanum* segregates first from the remaining taxa which agrees with the previously generated phenogram (Hawksworth and Wiens 1972) based on morphological, physiological, ecological, and host data. *A. douglasii* and *A. pusillum* are not shown to be closely related nor recent derivatives of the *Campylopodium* stock. The former taxon shows affinity with "Section vaginata," here including *A. vaginatum* ssp. *cryptopodium*, *A. vaginatum* ssp. *durangense*, *A. gillii*, and *A. divaricatum*. A Mexican taxon, *A. rubrum*, although somewhat transitional, groups more naturally with "Section vaginata" than with the *Campylopodium* group. Within this group, eleven taxa show high levels of genetic similarity (80% or greater) making species delimitations more difficult. Owing to morphological reductions and phenotypic convergence, phylogenetic relationships in these parasites have been obscured.

INTRODUCTION

The genus *Arceuthobium* is currently recognized as comprising 32 North American taxa with centers of species diversity in Northern California and the Sierras of Mexico (Hawksworth and Wiens 1972; 1977). The aim of this study was to obtain new sources of evidence to address taxonomic and evolutionary questions in 19 New World taxa of dwarf mistletoes.

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Electrophoresis has proven to be a powerful tool in delimiting plant and animal taxa at the generic and specific level. The advantages and shortcomings of this technique have been discussed (Avisé 1974; Gottlieb, 1977). This method of analysis was chosen primarily because it allows a sensitive assay of gene products (proteins and/or enzymes) across many gene loci and can be readily applied to numerous individuals sampled from natural populations. Crawford (1983) presents a convincing discussion of the value of this method over other chemosystematic approaches.

In parasitic plants such as *Arceuthobium*, reductions and convergences tend to obscure phylogenetic relationships (as measured by traditional morphological analyses) by limiting the number of characters, both vegetative and reproductive, available for study. The chances for "errors in assignment" (Kuijt 1969) thus become enormous. The taxonomy and classification of dwarf mistletoes has been the source of varied interpretations (Gill 1935; Kuijt 1955; Hawksworth and

Wiens 1972), yet none of these studies utilized biosystematic approaches involving crossing experiments or genetic analysis at the macromolecular level. For this reason electrophoresis seemed especially amenable to this taxonomically difficult group.

In contrast to the early work by Gill (1935), Hawksworth and Wiens (1972) do not delimit dwarf mistletoe taxa solely on the basis of host relationships. A major tenet of their system is that the mistletoes "maintain morphological integrity on separate hosts and are identifiable". Such a system is clearly an advancement over the previous one. For example, both *Arceuthobium vaginatum* ssp. *cryptopodum* and *A. cyanocarpum* may parasitize *pinus ponderosa*, yet these two taxa are quite distinct morphologically.

The relevance of the results of this study can be better understood given an initial introduction to the results of the phenetic analysis conducted by Hawksworth and Wiens (1972). In that study, characters involving morphology, physiology, host associations, and secondary compound chemistry were tabulated for 28 North American taxa and subjected to a Graph Theory Model of clustering (Wirth et al. 1966; Irwin and

Rogers 1967). The resulting dendrogram is reproduced in Figure 1. A summation of the phylogeny of the genus proposed by Hawksworth and Wiens (1972) is shown in Figure 2. Three letter abbreviations for dwarf mistletoe taxa shown in Figure 2 are explained in Table 1.

The 19 taxa utilized in this study are arranged according to the above taxonomic hierarchy of Hawksworth and Wiens (1972) and Kuijt (1955) as shown in Table 1. Hawksworth and Wiens (1972) proposed two subgenera, (*Arceuthobium* and *vaginata*, based primarily on the presence of verticillate secondary branching (the former subgenus) or flabellate secondary branching (the latter subgenus). Three sections within Subgenus *Arceuthobium* were also established (*vaginata*, *Campylopoda*, and *Minuta*). Section *vaginata* is considered to be the most primitive group whereas Section *Minuta* the most advanced owing to its diminutive shoot size and the occurrence of isophasic broom formation.

A particularly troublesome group within the genus, however, involves 13 taxa in Section *Campylopoda*, Series *Campylopoda* (as defined by Hawksworth and Wiens 1972). Nine of the 13 taxa were treated as forms of one variable species, *Arceuthobium campylopodum*, by Kuijt (1955)

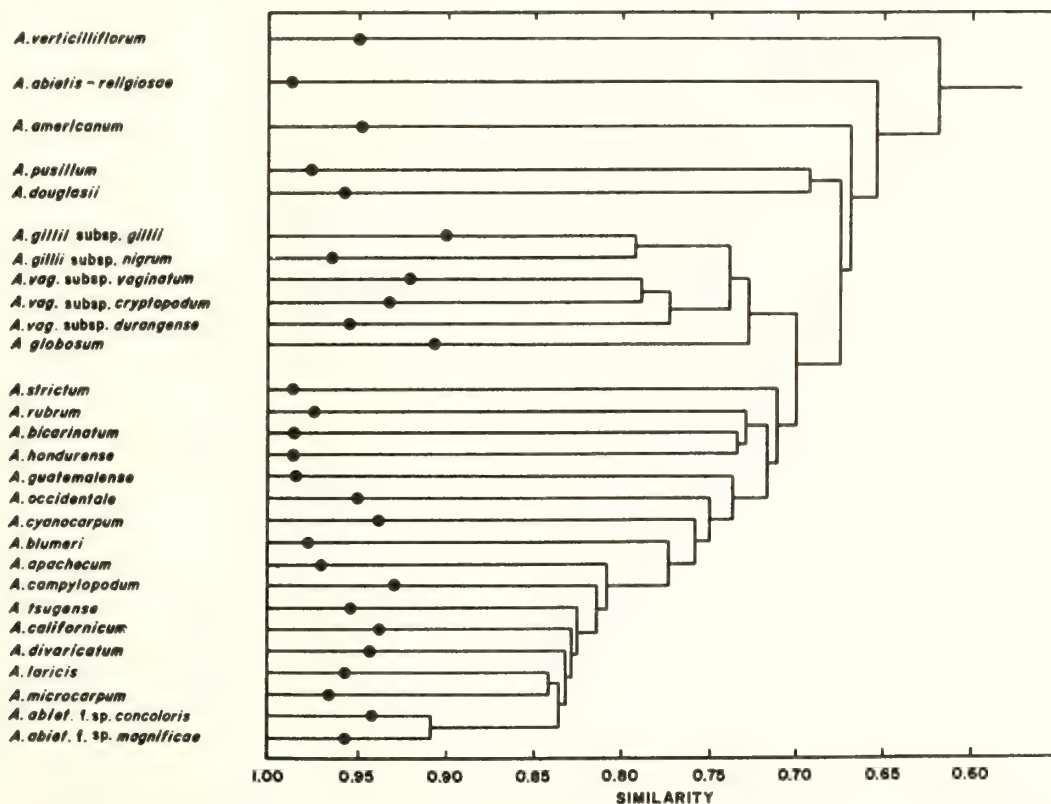


Figure 1.--Dendrogram showing the results of taximetric analyses of most New World dwarf mistletoes (reproduced from Hawksworth Wiens, 1972). The scale shows overall phenetic similarity based on combined analysis of 60 morphological, physiological, and host characters. The dot shows the level of intrataxon similarity. The further the dot from 1.0, the more variable the taxon.

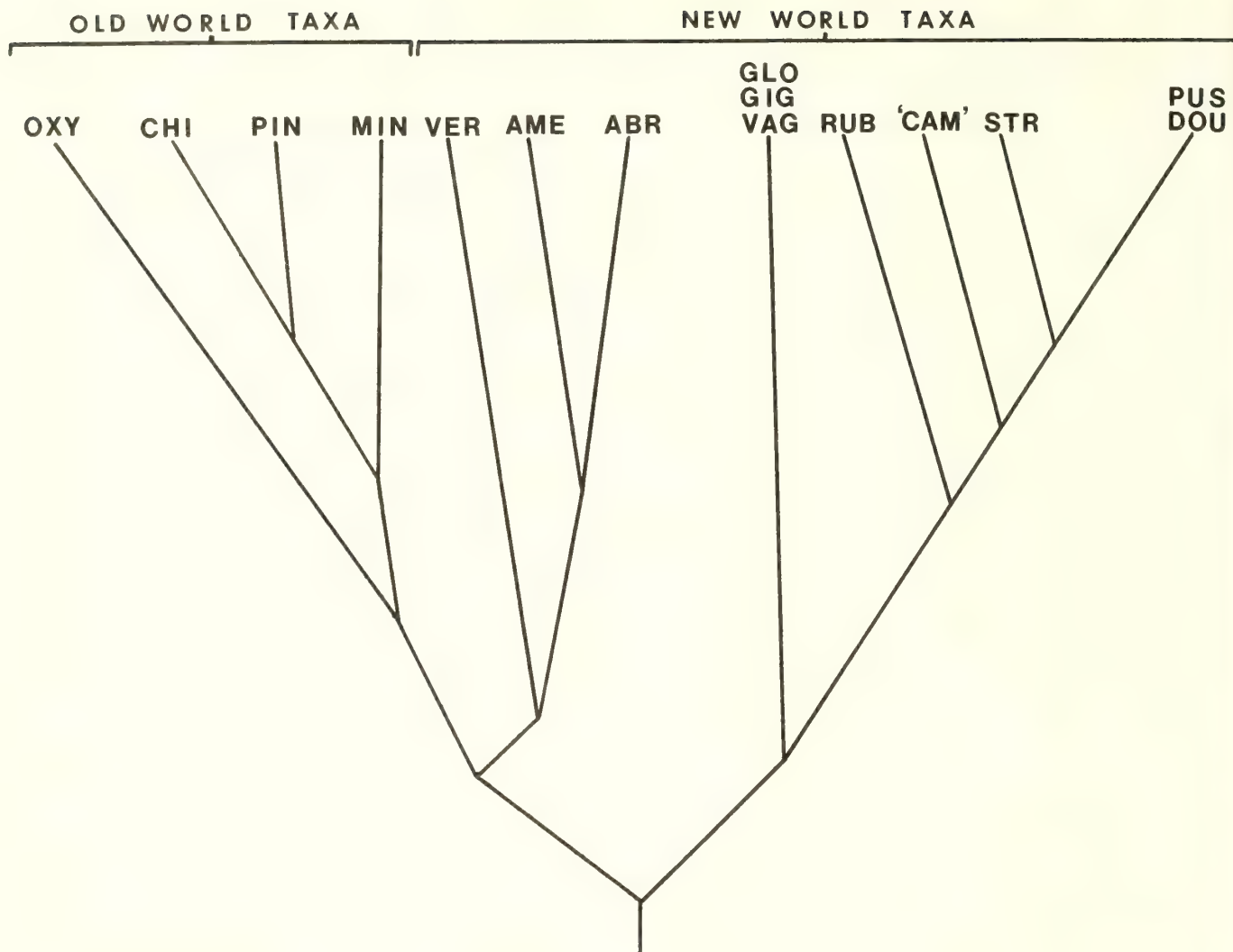


Figure 2.--presumed phyletic relationships among Old and New World *Arceuthobium*, redrawn from Hawksworth and Wiens (1972). New World taxon abbreviations not listed in Table 1 are: VER = *A. verticilliflorum*, ABR = *A. abietis-religiosae*. Old World taxa are: OXY = *A. oxycedri*, CHI = *A. chinense*, PIN = *A. pini*, and MIN = *A. minutissimum*.

(Table 1). Kuijt (1973) questioned whether the observed discontinuities warranted segregation at the specific level (as in the current system) or whether they would be best incorporated within an ecotype concept. The major discrepancy between the two systems involves the specific status of members of a large group (13 taxa) related to the ponderosa pine dwarf mistletoe *Arceuthobium campylopodum*. In view of the overall morphological similarity of the taxa in question, relationships can only be addressed by determining whether there is gene flow between these taxa in the natural, sympatric populations.

The degree of sympatry among dwarf mistletoes is often quite high. In areas such as the the Sierra Nevada of Northern California, as many as seven taxa can be

found within "gene exchange" distances. *Arceuthobium* is dioecious, therefore an obligate outcrosser. pollination appears to be mediated by both wind and (possibly primarily) insect vectors (penfield et al. 1976; Gilbert and punter, these proceedings). Anthesis is both temporally and spatially overlapping in many taxa, yet there exists no report of hybridization or polyploidy in the genus (Hawksworth and Wiens 1970; 1972). Unfortunately all taxa in the genus have $X=14$ as a base chromosome number (Wiens 1968), hence detection of hybrids utilizing cytology would be extremely difficult. With reference to *Arceuthobium campylopodum* and *A. occidentale*, Hawksworth and Wiens (1970) state "if mutual pollinating agents are available,

Table 1.-- Subgeneric classification of New World dwarf mistletoes used in this study according to Hawksworth and Wiens (1972) compared to Kuijt (1955)

Hawksworth and Wiens (1972)	Kuijt (1955)
I. Subgenus <u>Arceuthobium</u> No Sections Designated <u>A. americanum</u> (AME)	<u>A. americanum</u>
II. Subgenus <u>Vaginata</u> A. Section <u>vaginata</u> <u>A. gillii</u> (GIG) <u>A. vaginatum</u> ssp. <u>cryptopodum</u> (VAC) <u>A. vaginatum</u> ssp. <u>durangense</u> (VAD)	N.C. <u>A. vaginatum</u> N.C.
B. Section <u>Campylopoda</u> 1. Series <u>Campylopoda</u> <u>A. abietinum</u> f. sp. <u>concoloris</u> (ABC) <u>A. abietinum</u> f. sp. <u>magnificae</u> (ABM) <u>A. apachecum</u> (APA) <u>A. blumeri</u> (BLU) <u>A. californicum</u> (CAL) <u>A. campylopodum</u> (CAM) <u>A. cyanocarpum</u> (CYA) <u>A. divaricatum</u> (DIV) <u>A. laricis</u> (LAR) <u>A. microcarpum</u> (MIC) <u>A. occidentale</u> (OCC) <u>A. tsugense</u> (TSU) 2. Series <u>Rubra</u> <u>A. rubrum</u> (RUB)	<u>A. campylopodum</u> f. <u>abietinum</u> <u>A. campylopodum</u> f. <u>abietinum</u> N.C. N.C. N.C. <u>A. campylopodum</u> f. <u>campylopodum</u> <u>A. campylopodum</u> f. <u>cyanocarpum</u> <u>A. campylopodum</u> f. <u>divaricatum</u> <u>A. campylopodum</u> f. <u>laricis</u> <u>A. campylopodum</u> f. <u>microcarpum</u> <u>A. campylopodum</u> f. <u>campylopodum</u> <u>A. campylopodum</u> f. <u>tsugensis</u> N.C.
C. Section <u>Minuta</u> <u>A. douglasii</u> (DOU) <u>A. pusillum</u> (PUS)	<u>A. douglasii</u> <u>A. pusillum</u>

N.C. = Not Cited

genes should be exchanged if the plants are crossable."

Early in this study it was decided that "seeds" (used in the functional sense since members of the viscaceae lack true ovules) were the most practical tissue for use. Arceuthobium seeds are composed mainly of triploid endosperm (Bhandari and Nanda 1968) and have no true seed coat. Seeds are ideal for electrophoretic analysis because they 1) are easy to collect and transport in quantity, 2) can be stored for reasonably long periods of time under the proper conditions (Knutson 1971; Wicker 1974), 3) gave good enzyme activity in preliminary gel runs, and 4) can be harvested for analysis at the same developmental stage, thereby controlling "ontogenetic" enzyme variation (Scandalios 1974). In addition, seeds probably contain fewer secondary compounds than shoots. These compounds have been shown to be present in quantity in dwarf mistletoe shoots (Crawford and Hawksworth 1979) and are known to interfere with enzyme activity (Kelly and Adams 1977; Mitton, et al. 1979). Since the inception of the present study, Linhart (these proceedings) has successfully utilized dwarf mistletoe shoot material.

MATERIALS AND METHODS

Herbarium voucher specimens and seed material of 19 taxa of dwarf mistletoe were obtained in the fall of 1981 and 1982. pressed specimens were deposited at the Willard S. Turrell Herbarium at Miami University (MU). Although 24 of the 32 North American dwarf mistletoe taxa were observed in the field, not all had ripe fruits at the time of visitation, thus precluding their inclusion in the electrophoretic analysis. Seed viability was highest when collected during the "normal" period of dehiscence.

Table 2 lists the 40 populations utilized in this study with information on hosts and exact geographic location. The three letter abbreviations for each dwarf mistletoe taxon corresponds to the names shown in Table 1. These abbreviations will be used throughout the remainder of this paper. The full names of the host species (listed by numbers in Table 2) are given in Table 3.

All seeds were collected from dehiscing shoots into paper bags and stored in plastic bags at 2-4°C at ca. 80% relative humidity. Seeds from single female mistletoe shoots were collected in separate bags and attempts were made to obtain samples from 20 randomly selected

Table 2.-- Collection information for 40 populations of Arceuthobium used in this isozyme study.

Col. #	Taxon Abbr.	Host #*	Locality pop. Name, Co., State	Township, Range, Section
1.	1917 ABC	1	Cabbage patch, Calaveras, CA	T 7N R17E Sec. 30
2.	1940 ABC	1	Sumerhaven, Pima, AZ	T12S R15E Sec. 1
3.	1906 ABM	2	Greenhorn, Kern, CA	T24S R31E Sec. 36
4.	1910 ABM	2	Bass Lake, Madera, CA	T 6S R23E Sec. 18
5.	1916 ABM	2	Cabbage patch, Calaveras, CA	T 7N R17E Sec. 30
6.	1933 ABM	2	Bucks Lake, plumas, CA	T23N R 6E Sec. 11
7.	1939 APA	19	Bear Wallow, Pima, AZ	T12S R16E Sec. 5
8.	1948 APA	19	Hospital Flat, Graham, AZ	T 9S R24E Sec. 10
9.	1945 APA	19	Mt. Wrightson, Santa Cruz, AZ	T20S R14E Sec. 13
10.	1951 APA	19	Three Forks, Apache, AZ	T 6N R28E Sec. 34
11.	1937 BLU	19	Carr Canyon, Cochise, AZ	T23S R19E Sec. 1
12.	1930 CAL	13	Quincy, plumas, CA	T24N R10E Sec. 33
13.	1924 CAM	16	Emerald Bay, El Dorado, CA	T13N R17E Sec. 22
14.	1742 CAM	12	Forest, Sierra, CA	T19N R10E Sec. 19
15.	1750 CAM	16	Providence, plumas, CA	T25N R 8E Sec. 11
16.	1958 CYA	11	Lake Sabrina, Inyo, CA	T 8S R31E Sec. 29
17.	1973 CYA	11	Pingree-2, Larimer, CO	T 7N R73W Sec. 15
18.	1953 DIV	10	Red Hill, Greenlee, AZ	T 4N R31E Sec. 22
19.	1801 LAR	3	Malheur, Grant, OR	T15S R31E Sec. 15
20.	1950 MIC	7	Three Forks, Apache, AZ	T 6N R28E Sec. 34
21.	1947 MIC	4	Hospital Flat, Graham, AZ	T 9S R24E Sec. 3
22.	1962 OCC	18	Placerville, El Dorado, CA	T10N R11E Sec. 11
23.	1853 RUB	20	El Salto, Durango, Mexico	-----
24.	1927 TSU	15	Mt. Elwell, plumas, CA	T21N R12E Sec. 7
25.	1932 AME	8	Bucks Lake, plumas, CA	T23N R 7E Sec. 3
26.	1929 AME	8	Mt. Elwell, plumas, CA	T21N R12E Sec. 7
27.	1925 AME	8	Lake Tahoe, El Dorado, CA	T14N R17E Sec. 29
28.	1918 AME	8	Big Meadow, Calaveras, CA	T 7N R17E Sec. 33
29.	1955 DOU	21	Mt. Withington, Socorro, NM	T 4S R 7W Sec. 36
30.	1949 DOU	21	Turkey Flat, Graham, AZ	T 9S R25E Sec. 19
31.	1941 DOU	21	Bear Wallow, Pima, AZ	T12S R16E Sec. 5
32.	1938 GIG	14	Hitchcock, pima, AZ	T12S R16E Sec. 22
33.	1964 VAC	17	Pingree-1, Larimer, CO	T 8N R73W Sec. 25
34.	1876 VAC	17	San Antonio, Sandoval, NM	T19N R 3E Sec. 7
35.	1870 VAD	9	Puerto B.A., Durango, Mexico	-----
36.	1956 PUS	5	Waugochance, Emmet, MI	T39N R 5W Sec. 25
37.	1957 PUS	6	Levering, Emmet, MI	T38N R 4W Sec. 4
38.	1969 PUS	6	Big Falls, Koochiching, MN	T66N R25W Sec. --
39.	1970 PUS	6	Kerrick, Pine, MN	T44N R18W Sec. --
40.	1971 PUS	6	Cromwell, Carlton, MN	T49N R20W Sec. --

* Full specific names of hosts listed here by number are given in Table 3

host trees per population. This number was derived from a formula designed to determine optimal sample sizes when examining the genetics of forest trees (Brown and Moran 1981).

For germination the seeds were soaked in distilled water overnight or until the viscin coat was fully imbibed. The water was then replaced with 2% H₂O₂ and the seeds placed in a growth chamber set at 14°C with a 12:12 day to night cycle. Germination (extension of the radicle) was used as an indicator of viability of the endosperm (Figure 3C). All species of dwarf mistletoe utilized in this study germinated within 3-4 days under these conditions. Cold storage of certain

species (such as those within the Campylopodium group) for at least four weeks enhanced later seed germination.

To prepare the seeds for electrophoresis, the viscin coat and radicle (if necessary) was dissected away (Figures 3A and 3B) and the endosperm was then stored at -70°C. Owing to their small size (0.5-5.0 mg each), special methods were necessary to extract adequate enzyme samples from individual seeds. An additional disadvantage was that single seeds often provided only enough sample for 2-4 wicks, hence many seeds had to be prepared for a particular run and an individual seed could not be analyzed again. The latter problems were

Table 3.-- Hosts colonized by the dwarf mistletoes used in this study

1.	<u>Abies</u>	<u>concolor</u>
2.	<u>Abies</u>	<u>magnifica</u>
3.	<u>Larix</u>	<u>occidentalis</u>
4.	<u>Picea</u>	<u>engelmannii</u>
5.	<u>Picea</u>	<u>glauca</u>
6.	<u>Picea</u>	<u>mariana</u>
7.	<u>Picea</u>	<u>pungens</u>
8.	<u>Pinus</u>	<u>contorta</u> var. <u>murrayana</u>
9.	<u>Pinus</u>	<u>durangensis</u>
10.	<u>Pinus</u>	<u>edulis</u>
11.	<u>Pinus</u>	<u>flexilis</u>
12.	<u>Pinus</u>	<u>jeffreyi</u>
13.	<u>Pinus</u>	<u>lambertiana</u>
14.	<u>Pinus</u>	<u>leptophylla</u> var. <u>chihuahuana</u>
15.	<u>Pinus</u>	<u>monticola</u>
16.	<u>Pinus</u>	<u>ponderosa</u> var. <u>ponderosa</u>
17.	<u>Pinus</u>	<u>ponderosa</u> var. <u>scopulorum</u>
18.	<u>Pinus</u>	<u>sabiniana</u>
19.	<u>Pinus</u>	<u>stroboformis</u>
20.	<u>Pinus</u>	<u>teocote</u>
21.	<u>Pseudotsuga</u>	<u>menziesii</u>

circumvented by collecting large numbers of seeds and utilizing allele frequency data (not individual genotypes) for the systematic analysis.

For enzyme extraction, a plexiglass plate with 20 cylindrical wells and a steel pestle connected to a motor driven homogenizer was used. The plate was frozen at -70°C prior to use and kept on ice during grinding. Single seeds were ground in 35-40 μl of a 0.01 M Hepes buffer with 0.025 M 2-mercaptoethanol and 10% (w/v) polyvinylpyrrolidone (PVP-40). The crude extract was absorbed directly onto two Whatman #3 filter paper wicks measuring 4.0 X 9.0 mm. The plate with wicks was then frozen at -70°C and thawed just before loading the gels.

Enzyme separation was performed using horizontal starch gel (Sigma Co.) electrophoresis as described by Shaw and Prasad (1970). Eight enzyme systems were used in this study. 6-PGD (E.C. # 1.1.1.44), IDH (1.1.1.42), MDH (1.1.1.37), and G-6-PDH (1.1.1.49) were stained from citrate gels modified from Clayton and Tretiak (1972). For adequate resolution of 6-PGDH, 10.0 mg of NADP was added to the gel prior to degassing and 5.0 mg to each electrode tray prior to the gel run. ADH (E.C. # 1.1.1.1) and PGI (5.3.1.9) were stained from phosphate gels as described by Selander et al. (1971). PGM (E.C. # 2.7.5.1) and GDH (1.4.1.2) were stained from Tris-Borate gels as described by Ayala et al. (1972). The citrate gels were adjusted to pH 6.5 (gel) and 6.1 (electrode) using N-(3-aminopropyl)-morpholine.

The sample wicks were inserted into a slit in the gel and the gel run until a bromphenol blue marker dye migrated 11.0

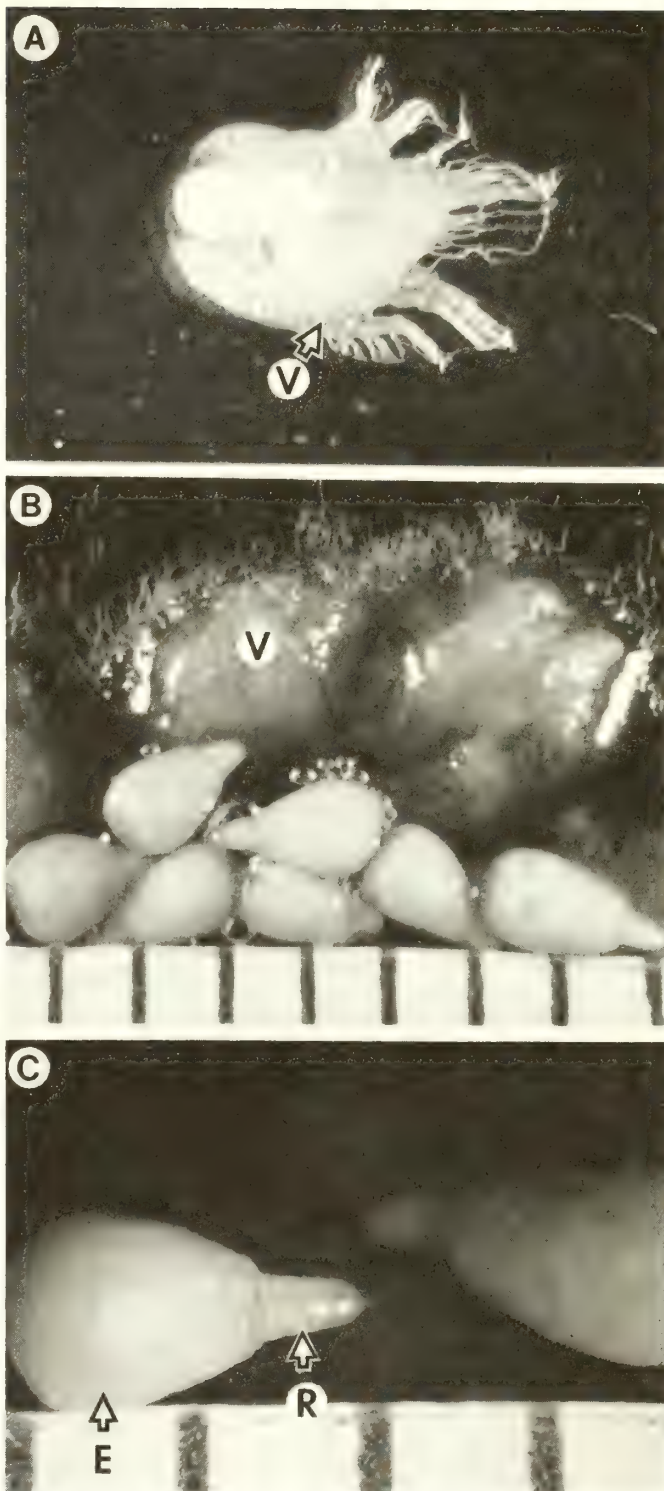


Figure 3a.--Ungerminated seed of Arceuthobium cyanocarpum dried onto a glass slide. 3b. Six day old germinating seedlings of above taxon (in 2% H_2O_2) with viscin coats removed. 3c. Closeup of seedlings from 3b without viscin coat. Scale in all figures in millimeters. E=endosperm, R=radicle, V= viscin coat.

cm. Enzyme staining for all systems was essentially as reported in Selander et al. (1971), Shaw and Prasad (1970), and Siciliano and Shaw (1976).

Bands for each enzyme locus were assigned relative mobility designations as compared to VAC seeds run as standards on each gel (assigned relative mobility values or "100"). For enzyme systems with two or more loci present on the gel, the most anodal locus was designated number one. Electromorph (= "allele") frequencies were tabulated for each locus and population and these frequencies subjected to analysis using BIOSYS-1, a FORTRAN IV computer program designed to analyze electrophoretically detectable genetic variation (Swofford and Selander 1981).

RESULTS

Eight enzyme systems representing eleven presumed loci gave interpretable results: 6-PGDH, IDH, MDH-2, MDH-3, G-6-PDH, PGI, ADH-1, ADH-2, PGM-1, PGM-2, and GDH. Allele (electromorph) frequency data were collected since one seed (individual) provided only enough sample for one gel. The mean number of individuals sampled per population for 6-PGDH was 37.4 with a range from 10 to 92. The sample sizes for most of the loci sampled among forty populations of dwarf mistletoes were usually well above ten individuals.

A data matrix of allele frequencies for 11 polymorphic loci for each of the 40 dwarf mistletoe populations is not reproduced here owing to its size (in

Nickrent, 1984). The number of alleles at all loci except G-6-PDH, ADH-2, and GDH exceeded 10. For 6-PGDH and PGI, greater than 20 alleles were detected for the 19 mistletoe taxa studied. For most loci there exists a common electromorph which occurs in high frequencies in many related taxa (e.g. 6-PGDH 150 in the *Campylopodum* complex). All loci reported here are polymorphic across all taxa, however GDH and G-6-PDH are often monomorphic within one species (the two most conservative systems).

Table 4 gives an estimation of genetic variability per taxon as measured by mean percent polymorphic loci per taxon and the mean number of alleles per locus per taxon. A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99. The mean percentage of loci polymorphic across all 19 taxa is 66.6, ranking dwarf mistletoes among the most genetically diverse dicotyledons examined electrophoretically. In comparison to averaged values for angiosperms and gymnosperms (Hamrick et al. 1981), *Arceuthobium* may be nearly twice as genetically variable as the average dicotyledonous plant. Some of the values in Table 4 should be interpreted with caution since the number of populations sampled for the taxon is small (one for BLU, CAL and others).

Mean levels of heterozygosity per taxon (Nei 1978) are not reported here because the sampled endosperm tissue is triploid, not diploid. The number of expected heterozygote classes is

Table 4.--Genetic variability for 19 taxa of dwarf mistletoe.

<i>Arceuthobium</i> Taxon	Number of Populations	% Polymorphic Loci Per Taxon	Mean Number of Alleles Per Locus Per Taxon
1. <i>A. abietinum</i> f. sp. <i>concoloris</i>	2	50.0	1.90
2. <i>A. abietinum</i> f. sp. <i>magnificae</i>	4	79.5	2.45
3. <i>A. americanum</i>	4	79.5	2.63
4. <i>A. apacheum</i>	4	59.0	2.18
5. <i>A. blumeri</i>	1	45.5	2.00
6. <i>A. californicum</i>	1	90.9	2.70
7. <i>A. campylopodum</i>	3	78.8	2.37
8. <i>A. cyanocarpum</i>	2	63.6	1.80
9. <i>A. divaricatum</i>	1	81.8	2.60
10. <i>A. douglasii</i>	3	72.7	2.70
11. <i>A. gillii</i>	1	54.5	2.50
12. <i>A. laricis</i>	1	63.6	1.70
13. <i>A. microcarpum</i>	2	59.1	2.10
14. <i>A. occidentale</i>	1	81.8	2.20
15. <i>A. pusillum</i>	5	50.9	1.78
16. <i>A. rubrum</i>	1	45.5	1.50
17. <i>A. tsugense</i>	1	72.7	1.90
18. <i>A. vaginatum</i> ssp. <i>cryptopodum</i>	2	63.6	2.60
19. <i>A. vaginatum</i> ssp. <i>durangense</i>	1	72.7	2.80
	Mean	66.6	Mean 2.23

necessarily elevated with increasing ploidy level thereby precluding the value of direct comparisons with diploids. The observed banding patterns for the triploid mistletoe endosperms conformed very well to expected patterns. Enzyme staining intensity and the number of bands present on a gel allowed accurate genotype assessments for most homozygote and heterozygote patterns seen. Interpretations of triploid enzyme banding patterns for monomeric and dimeric isozymes will be reported separately (Nickrent 1984).

Phenograms were generated using the unweighted pair group method with arithmetic averaging (UPGMA) as described in Sneath and Sokal (1973). The genetic similarity measure reported here is that of Nei (1978) shown in Figure 4. Other similarity measures such as by Rogers (1972) resulted in similar phenograms but differed in the percent standard deviation (Fitch and Margoliash 1967). The standard deviations for the above two measures were 56.717 and 22.454, respectively. The two measures differed primarily in the branching array for taxa within the

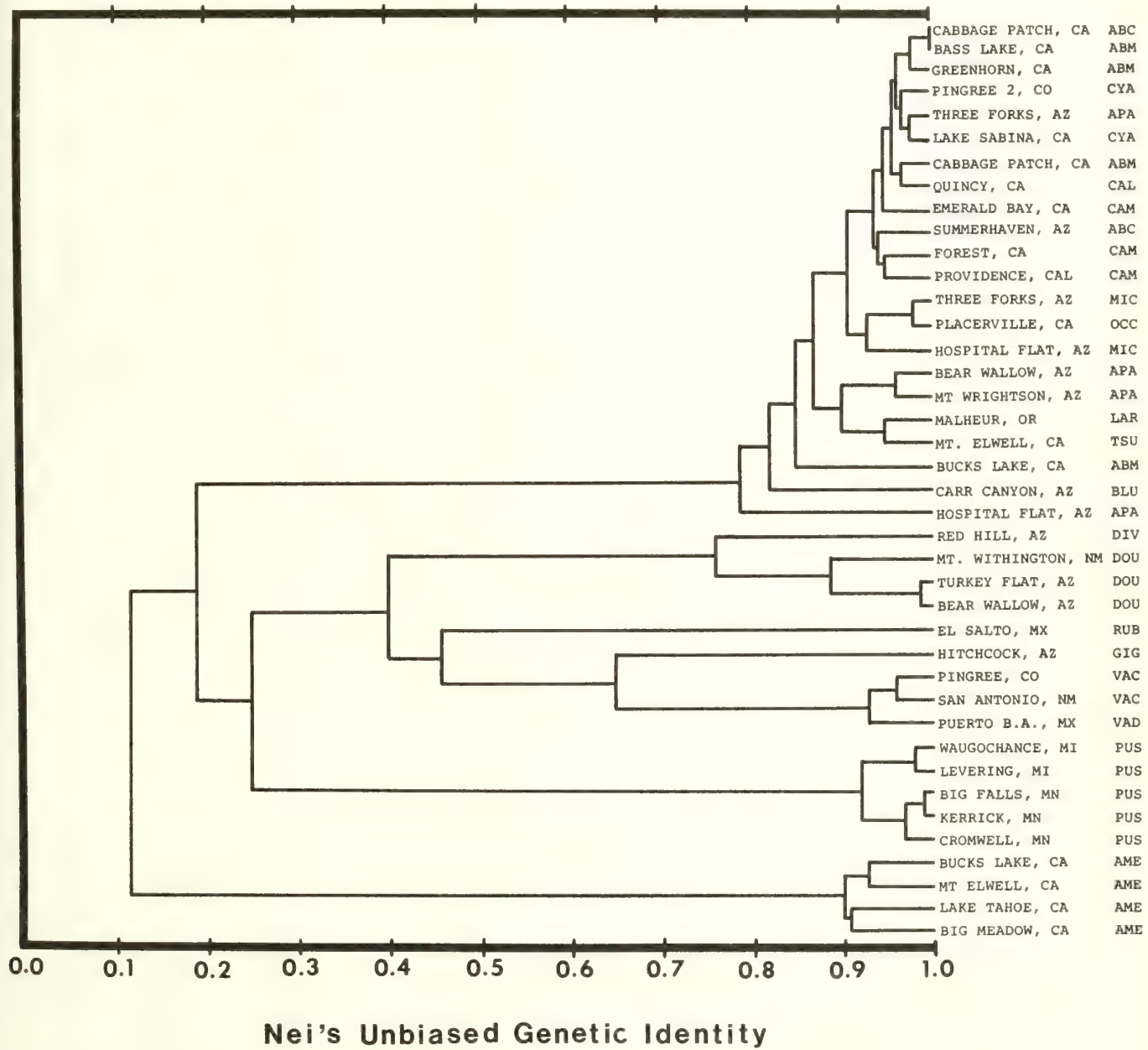


Figure 4.--UPGMA phenogram for the 40 dwarf mistletoe populations listed in Table 2 utilizing Nei's (1978) unbiased coefficient of genetic identity. See Table 1 for full taxonomic names here given three letter abbreviations.

Campylopodum complex. Also, Nei's (1978) measure showed a higher percent similarity for all taxa included in the analysis.

A matrix of genetic distance values (Nei 1978), averaged by species, is shown in Table 5. (mean distance values printed above, ranges below). The matrix for interpopulational genetic distances is not included owing to its size. Taxa were arranged according to the subgeneric, sectional, and series hierarchy outlined in Hawksworth and Wiens (1972) which is reproduced for the taxa under consideration here in Table 1. Ranges of the distance coefficients were used to examine the integrity of this arrangement by section (Table 6). An alternate sectional and series arrangement, based on the isozyme phenogram (Figure 4) is shown in Table 7. The means and ranges of the distance values, given this hierarchal arrangement, are shown in Tables 8 and 9.

The terms "section" and "series" are used in this paper for groupings as visualized from the isozyme results and carry no special taxonomic significance. The term "phenon" (Sneath and Sokal 1973) could be substituted for these terms. The categories were arbitrarily determined by examining the groupings of Figures 4 and then making subjective judgements as to the most natural subgeneric arrangement. The names given these categories are, in some cases, identical to those proposed by Hawksworth and Wiens (1972) even though the taxa included are not identical. Names such as "Series *Divaricata*" are proposed

only to accomodate the altered arrangement based on isozyme evidence.

When examining the sectional integrity of the arrangement shown in Table 6, the most heterogeneous group is Section *Minuta* with a mean distance value of 0.674 and ranges from 0.010-1.327. This contrasts with the mean intrasectional values for Section *Americana* (0.101) and *vaginata* (0.248). The highest value (2.372) for Section *Campylopodata* results from the inclusion of two taxa (*DIV* and *RUB*) which show greater affinity to other sections.

Tables 8 and 9 give the distance values for a sectional and series arrangement based on the isozyme phenograms. This arrangement reduces the variation in Section *Campylopodata* from a mean of 0.360 to 0.122. With this system of ranking, Section *vaginata* is the most heterogeneous group (mean of 0.690), owing mainly to the inclusion of *RUB*. This is illustrated by examining the intragroup integrity at the series level. Here, *RUB* is excluded from the remainder of the section and the distances for Series *Divaricata* and *vaginata* fall to 0.18 and 0.24 respectively. When all six series are examined, none of the intragroup values exceeds a distance 0.25.

A number of similarities and discrepancies appear when the phenetic analysis of Hawksworth and Wiens (1972) is compared to the present isozyme analysis. First, both methods segregate AME quite early from the remainder of the genus.

Table 5.--Interspecific genetic distance values (Nei 1978). Mean values above, ranges below.

	1	2	3	4	5	6	7	8	9	10
1. AME	0.101 (0.070-0.127)									
2. GIG	1.463 (1.236-1.705)	***** (*****-*****)								
3. VAD	1.683 (1.470-2.049)	0.336 (0.336-0.336)	***** (*****-*****)							
4. VAC	1.751 (1.475-2.124)	0.489 (0.448-0.529)	0.069 (0.056-0.082)	0.037 (0.037-0.037)						
5. OCC	2.670 (2.120-3.274)	1.449 (1.449-1.449)	1.114 (1.114-1.114)	1.201 (1.145-1.258)	***** (*****-*****)					
6. CYA	2.636 (2.184-3.116)	1.512 (1.459-1.565)	1.105 (1.089-1.121)	1.184 (1.125-1.227)	0.063 (0.057-0.070)	0.034 (0.034-0.034)				
7. BLU	2.944 (2.622-3.384)	1.641 (1.641-1.641)	0.974 (0.974-0.974)	1.008 (0.990-1.026)	0.196 (0.196-0.196)	0.173 (0.173-0.173)	***** (*****-*****)			
8. APA	2.526 (1.814-3.462)	1.356 (1.098-1.464)	1.039 (0.832-1.208)	1.127 (0.850-1.368)	0.181 (0.050-0.343)	0.110 (0.022-0.233)	0.281 (0.155-0.418)	0.130 (0.043-0.238)		
9. CAM	2.529 (2.064-3.215)	1.430 (1.427-1.433)	1.107 (1.028-1.148)	1.200 (1.061-1.298)	0.086 (0.069-0.101)	0.062 (0.029-0.104)	0.188 (0.169-0.200)	0.148 (0.043-0.309)	0.063 (0.050-0.082)	
10. TSU	3.063 (2.689-3.611)	1.588 (1.588-1.588)	1.150 (1.150-1.150)	1.215 (1.191-1.238)	0.203 (0.203-0.203)	0.136 (0.115-0.156)	0.285 (0.285-0.285)	0.119 (0.061-0.185)	0.192 (0.125-0.250)	***** (*****-*****)
11. CAL	2.565 (2.168-3.078)	1.397 (1.397-1.397)	1.038 (1.038-1.038)	1.119 (1.073-1.165)	0.030 (0.030-0.030)	0.044 (0.042-0.046)	0.121 (0.121-0.121)	0.135 (0.032-0.269)	0.059 (0.049-0.065)	0.150 (0.150-0.150)
12. DIV	1.463 (1.344-1.576)	1.007 (1.007-1.007)	0.580 (0.580-0.580)	0.597 (0.592-0.603)	1.995 (1.995-1.995)	2.019 (1.908-2.130)	1.535 (1.535-1.535)	1.947 (1.868-2.004)	1.898 (1.843-1.975)	2.372 (2.372-2.372)
13. LAR	2.756 (2.353-3.407)	1.474 (1.474-1.474)	1.081 (1.081-1.081)	1.161 (1.115-1.208)	0.130 (0.130-0.130)	0.142 (0.110-0.174)	0.259 (0.259-0.259)	0.174 (0.140-0.251)	0.166 (0.123-0.224)	0.052 (0.052-0.052)
14. MIC	2.525 (2.049-3.447)	1.395 (1.340-1.449)	1.071 (1.064-1.077)	1.148 (1.083-1.212)	0.039 (0.019-0.059)	0.089 (0.070-0.106)	0.252 (0.230-0.274)	0.201 (0.058-0.408)	0.140 (0.099-0.192)	0.202 (0.125-0.278)
15. ABC	2.637 (2.234-3.127)	1.491 (1.446-1.537)	1.077 (1.043-1.111)	1.158 (1.080-1.233)	0.080 (0.077-0.083)	0.044 (0.020-0.061)	0.118 (0.111-0.125)	0.133 (0.027-0.277)	0.067 (0.040-0.105)	0.184 (0.136-0.232)
16. ABM	2.557 (2.111-3.160)	1.437 (1.408-1.475)	1.055 (1.024-1.104)	1.150 (1.062-1.288)	0.094 (0.072-0.148)	0.066 (0.019-0.166)	0.186 (0.139-0.273)	0.131 (0.035-0.339)	0.083 (0.040-0.171)	0.135 (0.063-0.216)
17. RUB	2.562 (2.330-2.968)	0.784 (0.784-0.784)	0.733 (0.733-0.733)	0.777 (0.753-0.800)	1.229 (1.229-1.229)	1.248 (1.244-1.253)	1.043 (1.043-1.043)	1.257 (1.121-1.433)	1.255 (1.122-1.359)	1.231 (1.231-1.231)
18. DOU	1.465 (1.292-1.732)	1.166 (1.127-1.194)	0.816 (0.721-0.874)	0.826 (0.668-0.913)	2.375 (2.216-2.638)	2.164 (1.970-2.566)	1.505 (1.412-1.671)	2.229 (1.985-2.693)	2.096 (1.688-2.554)	2.331 (2.065-2.793)
19. PUS	1.920 (1.528-2.255)	1.552 (1.438-1.666)	1.354 (1.258-1.469)	1.423 (1.290-1.638)	1.912 (1.687-2.182)	1.952 (1.566-2.379)	2.105 (1.734-2.459)	1.766 (1.454-2.037)	1.825 (1.462-2.191)	2.240 (2.048-2.436)

Table 6.--Distance coefficients (Nei 1978) averaged by section*

Section	# Pops	1	2	3	4
1. Americana	4	0.101 (0.070-0.127)			
2. Vaginatum	4	1.662 (1.236-2.124)	0.248 (0.037-0.529)		
3. Campylopoda	24	2.564 (1.344-3.611)	1.167 (0.580-1.641)	0.360 (0.005-2.372)	
4. Minuta	8	1.750 (1.292-2.255)	1.239 (0.668-1.666)	1.946 (0.218-2.850)	0.674 (0.010-1.327)

*Sectional arrangement according to Hawksworth and Wiens (1972)

Also, both studies suggest that the vaginata group exhibits more variation, both morphological and genetic, than Section Campylopoda. The isozyme analysis does not, however, support the placement of DOU and PUS together in one Section (Minuta). Also, the pinyon dwarf mistletoe, DIV, segregates most closely with DOU, not the Campylopoda complex as suggested by the morphometric analysis. Arceuthobium rubrum (RUB), placed within its own Series of Section Campylopoda by Hawksworth and Wiens (1972) clusters with a group of three taxa generally representing Section vaginata. It is of interest that the morphometric analysis (Figure 1) shows this taxon (with A. strictum, which was not included in this study), having greater affinity with Section vaginata than any other members of Section Campylopoda.

The second major dichotomy of the genus based on isozyme evidence segregates those members placed in Section Campylopoda, Series Campylopoda by Hawksworth and Wiens (1972). The clustering patterns for those dwarf mistletoes included within Series Campylopoda do not support segregation of separate species. Ten taxa (ABC, ABM,

APA, CAL, CAM, CYA, LAR, MIC, OCC, and TSU) included in this group share a high degree of genetic similarity (greater than 80%). Six of these ten taxa (ABC, ABM, APA, CAM, CYA, and MIC) are represented in this study by more than one population, however the cluster analysis does not unambiguously group them together. Some tendency to group according to species, as defined by Hawksworth and Wiens (1972), is seen in some populations of Arceuthobium abietinum s. l., CAM, and APA.

These discrepancies in grouping the taxa considered species within the Campylopoda complex stand in sharp contrast to the well resolved species segregating in the lower half of the phenograms shown in Figure 4. Arceuthobium vaginatum s.l., AME, DIV, DOU, GIG, PUS, and RUB are formed at specific identity values of ca. 75%. The two subspecies of A. vaginatum, VAC and VAD, segregate at ca. 92% similarity using Nei's (1978) index. Many of the populations considered separate species according to Hawksworth and Wiens (1972) show equally high (75% or greater) levels of identity.

Table 5.--Interspecific genetic distance values (Nei 1978). Mean values above, ranges below

	11	12	13	14	15	16	17	18	19
11. CAL	***** (*****-*****)								
12. DIV	1.886 (1.886-1.886)	***** (*****-*****)							
13. LAR	0.112 (0.112-0.112)	2.122 (2.122-2.122)	***** (*****-*****)						
14. MIC	0.075 (0.061-0.089)	2.030 (1.987-2.074)	0.147 (0.094-0.199)	0.079 (0.079-0.079)					
15. ABC	0.030 (0.020-0.040)	1.917 (1.898-1.936)	0.177 (0.140-0.213)	0.124 (0.108-0.155)	0.037 (0.037-0.037)				
16. ABM	0.054 (0.026-0.116)	1.967 (1.950-2.005)	0.122 (0.048-0.170)	0.140 (0.083-0.241)	0.074 (0.005-0.208)	0.077 (0.017-0.131)			
17. RUB	1.199 (1.199-1.199)	1.423 (1.423-1.423)	1.160 (1.160-1.160)	1.090 (1.008-1.172)	1.230 (1.194-1.266)	1.209 (1.154-1.273)	***** (*****-*****)		
18. DOU	2.146 (1.983-2.468)	0.279 (0.218-0.324)	2.409 (2.181-2.850)	2.546 (2.352-2.744)	2.111 (1.921-2.466)	2.171 (1.890-2.711)	1.408 (1.392-1.436)	0.080 (0.010-0.120)	
19. PUS	1.808 (1.548-2.083)	1.156 (1.053-1.239)	2.027 (1.857-2.256)	1.912 (1.606-2.206)	1.710 (1.351-2.096)	1.901 (1.601-2.225)	2.194 (1.892-2.463)	1.204 (1.113-1.327)	0.057 (0.014-0.121)

Table 7.--Subgeneric classification of New World dwarf mistletoes used in this study based on isozyme evidence.

A. Section <u>Arceuthobium</u> *	
	<u>A. americanum</u>
B. Section <u>pusilla</u>	
	<u>A. pusillum</u>
C. Section <u>Campylopoda</u>	
	<u>A. abietinum</u> f. sp. <u>concoloris</u>
	<u>A. abietinum</u> f. sp. <u>magnificae</u>
	<u>A. apachecum</u>
	<u>A. blumeri</u>
	<u>A. californicum</u>
	<u>A. campylopodum</u>
	<u>A. cyanocarpum</u>
	<u>A. laricis</u>
	<u>A. microcarpum</u>
	<u>A. occidentale</u>
	<u>A. tsugense</u>
D. Section <u>vaginata</u>	
1. Series <u>vaginata</u>	
	<u>A. gillii</u>
	<u>A. vaginatum</u> ssp. <u>cryptopodum</u>
	<u>A. vaginatum</u> ssp. <u>durangense</u>
2. Series <u>Rubra</u>	
	<u>A. rubrum</u>
3. Series <u>Divaricata</u>	
	<u>A. divaricatum</u>
	<u>A. douglasii</u>

* The categories "Section" and "Series" and their names carry no special taxonomic meaning in this study (see text).

DISCUSSION

The above evidence indicates that the two classifications, one based on morphology, physiology, and host information (Hawksworth and Wiens 1972), and the present isozyme analysis, provide different interpretations of relationships in the genus. This is not unusual for it has been well established that taxonomic data derived from disparate sources can often lead to entirely different classifications (Mayr 1981; Patton and Avise 1983).

Three major difficulties of biological classification are that 1) we are constrained by the evidence at hand (i.e. extant taxa and fossils) and common ancestry must therefore be presumed, 2) evolutionary change over time may occur at very different rates for different taxa, and 3) we may or may not be successful in attempting to use any one system for both information storage and retrieval and as a basis for biological generalizations and explanations (Lehman 1971; Kavanaugh 1977; Mayr 1981; and Jensen 1983). At least three major schools of thought currently attempt to unambiguously determine the degree of relatedness between taxa, the phenetic, cladistic, and evolutionary taxonomic methods (Mayr 1981). Although there are strong proponents for both the purely phenetic and purely cladistic schools, biologists working with a variety of groups, each with its own evolutionary peculiarities, seem to be striving toward a consensus where information from each method can be incorporated to provide a suitable, workable evolutionary classification. This position has been advanced by Grant (1982) for plants and Mayr (1969; 1981) for animals. Mayr (1981) states that the goal of the evolutionary taxonomist is to "...construct classifications that reflect both of the two major evolutionary processes, branching and divergence (cladogenesis and anagenesis)".

Two examples of apparent morphological convergence involve DIV compared with the Campylopodum complex and DOU compared with PUS. The pinyon pine dwarf mistletoe interestingly shows affinity with DOU, the principle parasite of Douglas fir. Pinyon pines are generally lower elevation species in the western U.S., hence the degree of sympatry between DIV and most other dwarf mistletoe taxa is low. The placement of DIV nearer to DOU than to any taxon in the Campylopodum complex is a radical departure from the treatment in Hawksworth and Wiens (1972).

Table 8.--Distance coefficients (Nei 1978) averaged by section*

Section	# Pops	1	2	3	4
1. Americana	4	0.101 (0.070-0.127)			
2. Pusilla	5	1.920 (1.528-2.255)	0.057 (0.014-0.121)		
3. Campylopoda	22	2.614 (1.814-3.611)	1.881 (1.351-2.459)	0.122 (0.005-0.418)	
4. Vaginata	9	1.675 (1.236-2.968)	1.413 (1.053-2.463)	1.621 (0.832-2.850)	0.694 (0.010-1.436)

*Sectional arrangement according to isozyme evidence.

Table 9.--Distance coefficients (Nei 1978) averaged by series*

Series	# Pops	1	2	3	4	5	6
1. Americana	4	0.101 (0.070-0.127)					
2. Pusilla	5	1.920 (1.528-2.255)	0.057 (0.014-0.121)				
3. Campylopoda	22	2.614 (1.814-3.611)	1.881 (1.351-2.459)	0.122 (0.005-0.418)			
4. Vaginata	4	1.662 (1.236-2.124)	1.438 (1.258-1.666)	1.206 (0.832-1.641)	0.248 (0.037-0.529)		
5. Divaricata	4	1.465 (1.292-1.732)	1.192 (1.053-1.327)	2.137 (1.412-2.850)	0.855 (0.580-1.194)	0.180 (0.010-0.324)	
6. Rubra	1	2.562 (2.330-2.968)	2.194 (1.892-2.463)	1.210 (1.008-1.433)	0.768 (0.733-0.800)	1.412 (1.392-1.436)	***** (*****-*****)

*Series arrangement according to isozyme evidence.

***** Only one population included.

It could be stated that biochemical divergence occurred in DIV (from the Campylopodum group) and that similarity to DOU is coincidental, i.e. the bands which migrate to the same position on a gel are "electromorphs" and do not represent homologous proteins. Electromorphs appearing the same among different taxa may, under altered electrophoretic conditions, prove to be different (Coyne et al. 1979). In this case, however, when the total number of shared electromorphs is examined, a more reasonable explanation is that similarity is by descent. Both DIV and DOU are fixed for GDH-66 which is absent in all other taxa. In addition, they share: 6-PGD-65, 6-PGD-100, PGI-154, PGI-178, ADH-1-100, ADH-1-132, ADH-1-164, ADH-2-100, PGM-1-76, PGM-1-97, PGM-2-97, PGM-2-100, G-6PDH-100, MDH-2-76, MDH-2-100, and MDH-3-205. The probability of independently evolving this complement of electromorphs is very remote.

The phylogenetic relationships between AME, PUS, and DOU may not be as distant as is suggested by Figure 2 from Hawksworth and Wiens (1972). In this figure it is surprising to see Section Minuta as being the most recently derived component of all the members of Subgenus vaginata, especially since these taxa do show association on the morphometric dendrogram (Figure 1).

Despite the early segregation of AME from all other taxa utilized in this isozyme study (supporting its retention in a separate subgenus), the affinities of this species to Section Minuta (specifically PUS) still remains in question. These three taxa (AME, DOU, PUS) share the following features:

- 1) spring flowering
- 2) an asynchrony of male and female meiosis
- 3) primarily isophasic broom formation
- 4) extensive geographic ranges
- 5) high tendencies to "cross-over" (i.e. colonize secondary host species)
- 6) specific fungal hyperparasite colonization (Wallrothiella arceuthobii; Kuijt 1963).
- 7) highest mean number of electromorphs (28 for AME, 29 for DOU compared to a mean of 23.6 across 11 loci for all 19 taxa used in this isozyme analysis).

Given the criterion of secondary branching type (i.e. verticillate vs. flabellate), two subgeneric categories could be established irrespective of any other characters. Kuijt (1970), however, pointed out that strict adherence to the type of secondary branching pattern when delimiting subgenera is not suitable, especially with Old World members such as Arceuthobium minutissimum. The latter species is placed in Subgenus Arceuthobium by Kuijt (1970) and Hawksworth and Wiens (1972) even in the absence of evidence on secondary branching (owing to the extreme morphological reduction). A similar situation may well exist for the eastern dwarf mistletoe, PUS, where only primary branching has been reported. In addition, the frequency of verticillate or flabellate branching can be a variable

character. Mark and Hawksworth (1981) noted that CAM may show 0-18% verticillate branching and OCC 0-10%. This variable condition was also noted in VAC and CYA. The degree of verticillate secondary branching in various members of subgenus Arceuthobium can vary tremendously between taxa. This character was used by Hawksworth and Wiens (1976) to segregate A. juniperi-procerae (native to Africa) from A. oxycedri (wide ranging in Europe and Asia). The former taxon displays less than 3% verticillate secondary branching whereas the latter shows ca. 45% whorled arrangement.

The phenetic analysis based on isozyme evidence segregates four major groups at the 0.3% similarity level Figure 4). This arrangement by section and series, based upon the isozyme phenograms, provides a more equitable hierarchy, given electrophoretic distance values, than the arrangement according to Hawksworth and Wiens (1972). The affinities of RUB with Section vaginata is shown with both the isozyme analysis (Figure 4) and the morphological analysis (Figure 1), although more strongly with the former measure. The most variable section within this arrangement is vaginata. This agrees with the results of the morphometric analysis of Hawksworth and Wiens (1972).

Defining a species in the Campylopodum complex is difficult because of the overall high degree of genetic similarity. Since species limits are well defined in some cases (AME, DOU, PUS, etc.) but not in others, it is proposed that either 1) the complex does not contain distinct species, or 2) the complex is composed of closely related (sibling) species, possibly undergoing more rapid (and more recent) radiation than other members of the genus. The evidence presented here does not discount the scheme of relationships within the Campylopodum complex as proposed by Kuijt (1955) (Table 1). As has long been recognized, host relationships are crucial to developing an understanding of speciation in this group. When commenting that evolutionary divergence is independent of reproductive isolation, Levin (1979) said species are "the total assemblage of adaptive peaks with continuity between the peaks." For the Campylopodum complex, these peaks may well correspond to the major host species.

It would be desirable, then, to utilize all of the information at hand in order to construct a model phylogeny for this interesting genus of parasites. Whether the methodology involves cladistic or phenetic techniques, the most rational approach to dwarf mistletoe classification would be an attempt to use the information from each area in the process of synthesizing a phylogeny. The following conclusions can be derived from the results of this study:

1) Arceuthobium shows very high levels of genetic variability.

2) AME represents the most primitive New World member of the genus included in this study.

3) DOU and PUS are not recent derivatives from the Campylopodum stock. The phylogenetic affinities of the former species are with Section vaginata.

4) DOU and PUS, as shown by isozyme evidence, are not closely related to one another.

5) DIV appears to reside more naturally with Section vaginata than with Section Campylopada.

6) The affinities of VAC, VAD, and GIG are supported by the previous analysis of Hawksworth and Wiens (1972) and the present isozyme study. This group is both morphologically and genetically more variable than other members of the genus.

7) Eleven taxa within the Campylopodum complex show high levels of genetic similarity (ca. 80%). These are: ABC, ABM, APA, BLU, CAL, CAM, CYA, LAR, MIC, OCC, and TSU. In comparison to species limits of AME, DOU, and PUS, these taxa show greater inter- taxon similarity.

8) The Mexican taxon, RUB, appears to occupy a transitional position between the Campylopodum and vaginatum groups.

The placement of DIV either with Section vaginata or Campylopada remains the major discrepancy between the former and present proposed classifications. This impasse can only be resolved by broadening the scope of genetic investigation to include more Mexican and Central American taxa such as Arceuthobium pendens. Other Mexican taxa central to developing an understanding of phylogenetic relationships in this genus include: A. abietis-religiosae, A. verticilliflorum, A. gillii ssp. nigrum, A. vaginatum ssp. vaginatum, A. strictum, and A. globosum. The inclusion of Old World taxa would also be extremely helpful, especially to establish the proper placement of such taxa as A. pusillum at the subgeneric level.

Questions raised by this isozyme study involving the evolution and taxonomy of certain component taxa include:

1) What is the evolutionary and biogeographic relationship between DIV and DOU?

2) What is the phylogenetic status of PUS and its relationship to AME,

especially in reference to subgeneric concepts in the genus?

3) What is the specific status of component taxa in the closely related *Campylopodum* complex? Are these taxa very recently evolved (or evolving) species segregating along host lines? If so, what are the selective forces driving this radiation?

4) Given high levels of genetic variability, the evolutionary potential of these parasites is quite great. How must this influence our concepts of speciation and pathogenicity in *Arceuthobium* with respect to effective control?

5) How must the current classification system be modified to incorporate this additional information on genetic relationships?

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Genetic Variability in the Dwarf Mistletoes *Arceuthobium vaginatum* subsp. *cryptopodum* and *A. americanum* on their Primary and Secondary Hosts¹

Yan B. Linhart²

Abstract.--Electrophoretic analyses of genetic variation have been carried out on *Arceuthobium americanum* and *A. vaginatum* subsp. *cryptopodum*. Several polymorphic loci have been detected in both. A comparison of *A.v. cryptopodum* populations growing on *Pinus ponderosa*, its primary host, and *P. contorta*, a secondary host, indicated significant heterogeneity of allele frequencies between the two populations at two of the three loci tested. There was no evidence of differentiation at one locus in *A. americanum* whose primary host is *P. contorta* and secondary host is *P. ponderosa*.

INTRODUCTION

Dwarf mistletoes of the genus *Arceuthobium* are common parasites on pines and other conifers of the Rocky Mountains. Each of the 3 main pine species in northern Colorado is the primary host of an *Arceuthobium* species. *Pinus ponderosa* is parasitized by *A. vaginatum* subsp. *cryptopodum*, *P. contorta* is parasitized by *A. americanum* and *P. flexilis* is parasitized by *A. cyanocarpum*. However, all three of these *Arceuthobium* species also grow on occasion on the "wrong" two pine species which then can serve as secondary hosts. The frequency with which this happens is variable but all nine possibilities have been seen in the field (Hawksworth and Peterson 1959, Hawksworth et al. 1975, Hawksworth 1978).

As this symposium attests, a great deal is known about the ecology, systematics and destructive features of *Arceuthobium*. The extent of its variability and other features of its genetics are less well known and are in need of study for practical and theoretical reasons. The practical reasons are based on the fact that it is the most damaging disease of conifers in many regions in western North America and Canada (Hawksworth 1978, 1983). Methods of reducing damage levels depend on proper biological management including thinning and pruning

(Scharpf and Parmeter 1978) and can benefit from a better understanding of the biology of the genus. The theoretical reasons include the fact that little is known about the evolutionary genetics of parasitic angiosperms (Kuijt 1969, Calder and Bernhardt 1983) and how they compare to other angiosperms in terms of their levels of variability (Hamrick et al. 1979), extent of geographic variation and population differentiation (Stebbins 1950, Endler 1977), and the possibilities of co-evolution with their hosts (Futuyma and Slatkin 1983).

The primary objective of this paper is to discuss preliminary analyses of electrophoretically-detectable genetic variation in *A.v.* subsp. *cryptopodum* and *A. americanum*. Two questions are asked:

1) Which loci are variable in which species and under which electrophoretic conditions. This will be useful in determining methodology of future studies.

2) Are there any differences between the genetic constitutions of a given *Arceuthobium* species on its primary host and on a secondary host? This question is useful in the context of determining whether there is a possibility of host race formation. This is observed in many insects which can feed upon a variety of plant hosts and show significant genetic differentiation as a result.

MATERIALS AND METHODS

Shoot samples of *A. vaginatum* subsp. *cryptopodum* (henceforth *A.v.*) and *A. americanum* (henceforth *A.a.*) were collected on *Pinus*

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ponderosa (P.p.) and Pinus contorta (P.c.). In addition A.v. were collected on P. flexilis (P.f.). All collecting was done in a mixed stand containing all three species in an area north of Nederland, Colorado, U.S.A. (Lat. 39° 57'N., Long. 105° 35'W.) at an elevation of 2600 m. Collecting was not done randomly. Efforts were made to collect colonies from a variety of locations on a given tree. Also, colonies were collected from a variety of trees. Three to six colonies were collected from most single trees, with a maximum of 16 A.v. from one P.c. because P.c. with A.v. infestations were difficult to find. Both species were in flower, and the sex could be determined for all colonies of A.a. and many colonies of A.v.

The shoot samples were brought back to the laboratory and, within one day, ground in liquid N and then mixed with a buffer, following methods described in Mitton et al. (1979). The system in which the samples were run include the discontinuous buffer described in Mitton et al. (1977) and the continuous buffer described in King and Dancik (1983).

Allele frequencies were compared between populations growing on either host; they were also compared between sexes. Sample sizes used to determine allele and genotype frequencies for a given category, i.e. host population or sex, are 39 to 47. Differences were tested with the chi-square test of Workman and Niswander (1970).

RESULTS AND DISCUSSION

Methodology

For any given protein, the same buffer system gave proper resolution for material from all species of mistletoe sampled (i.e. A.a., A.v. and a few A. cyanocarpum collected from P.f.).

The buffer we have used most commonly for ponderosa pine tissue and described in Mitton et al. (1977) was especially useful for the following enzymes. The list also indicates magnitude of genetic variability as H = High, meaning there are at least two alleles with the most common allele at frequency $P \leq 0.90$ or L = Low with $P > 0.95$. Alcohol Dehydrogenase (A.D.H.) two loci, the faster one is H, the slower one is L. Glutamate Dehydrogenase (G.D.H.) L; Phosphoglucose Isomerase (P.G.I.) H; Peroxidase (PER) several loci, one H others L.

The continuous buffer of King and Dancik (1983) was especially good for the following enzymes. Aconitase (ACO) L; Isocitrate Dehydrogenase (I.D.H.) L; 6-Phosphogluconate Dehydrogenase (6-P.G.D.H.) L; Malate Dehydrogenase (M.D.H.) H; Phosphoglucumutase (P.G.M.) 2 loci, both H.

Results are reported here on only a few of these loci. In all cases the loci are presumptive because no control-pollinations were done and no comparisons were done between parents and progenies. However, they are considered to be

loci based on extensive previous experience with these enzymes in many plant species both in our laboratory and elsewhere (Hamrick et al. 1979). Appropriate controls were run with fresh versus older, refrigerated tissues, and with several samples of varying developmental sizes from one colony. Furthermore all loci showed distributions of genotypes which were very close to those expected under Hardy-Weinberg equilibrium.

Variation in A. americanum

A. americanum was abundant on P. contorta in the stand sampled. Most trees had at least a few colonies. A. americanum also colonized P. ponderosa readily. Because an effort was made to collect balanced samples of both ♀ and ♂, the sex ratio cannot be determined from these samples, but both sexes were common on both pines. Patterns of genetic variation in A.a. are summarized in Table 1. There are no significant differences in allele frequencies between sexes or between A.a. on the two hosts. The lack of differentiation in allele frequencies parallels the lack of differentiation at the morphological level.³ Observed genotypic frequencies do not differ significantly from those expected under Hardy-Weinberg equilibrium for either sex or for populations collected from the two hosts.

Table 1.--Frequency of two most common alleles at the PGI locus in A. americanum growing on either of two hosts (C = P. contorta; P = P. ponderosa) or of either sex. Chi square tests the difference between hosts or sexes, and P indicates significance level.

Locus and alleles	Host		Sex	
	C	P	♀	♂
P.G.I. Frequency				
Allele 1	0.13	0.10	0.05	0.17
Allele 3	0.81	0.78	0.83	0.76
χ^2 (P)	2.63(P<0.20)		1.23(P>0.20)	

Variation in A. vaginatum

A. vaginatum is common on P. ponderosa in the stand sampled, but, in contrast to the frequent occurrence of A.a. on the "wrong" host, A.v. is not very common on P. contorta in this area. Few P.c. have A.v. and when they do have it, they support few colonies. A.v. was also found on one P. flexilis. As in A.a., both sexes were common on both pines.

³Hawksworth, Frank G. 1984. Personal conversation. USDA Forest Service, Rocky Mountain Forest Experiment Station, Ft. Collins, Colo.

There are significant differences in allele frequencies at the P.G.I. and A.D.H. loci between A.v. on P.p. versus P.c. (Table 2). This differentiation parallels the differentiation in morphology and color between A.v. on P.p. versus P.c. as noted by Hawksworth.³

Table 2.--Frequency of most common allele(s) at three loci in *A. vaginatum* subsp. *cryptopodum* growing on either of two hosts or of either sex. Chi square tests the difference between hosts or sexes, and P indicates significance level.

Locus and allele(s)	Host		Sex	
	C	P	♀	♂
P.G.I. Frequency of most common alleles				
Allele 2	0.26	0.10	0.20	0.15
Allele 4	0.33	0.40	0.39	0.32
Allele 5	0.20	0.29	0.25	0.38
χ^2 (P)	14.37(P<0.01)		1.10(P>0.50)	
A.D.H. Frequency				
Allele 2	0.78	0.94	0.69	0.82
χ^2 (P)	8.60(P<0.005)		0.36(P>0.50)	
PER Frequency				
Allele 2	0.65	0.63	0.52	0.67
χ^2 (P)	0.36(P<0.50)		3.71(P=0.06)	

There are no statistically significant differences in allele frequencies between sexes of A.v. at two loci, though values are close to significance at the PER locus.

Observed genotypic frequencies do not differ significantly from those expected under assumptions of Hardy-Weinberg equilibrium for any locus, either sex or either host population.

The sample of A.v. from a single P.f. host consisted of five colonies only. The plants did not differ strikingly in either morphological or electrophoretic phenotypes from the other host populations.

GENERAL DISCUSSION

The *Arceuthobium* species tested so far are quite variable genetically in that more than one third of the loci tested to date are polymorphic. In very detailed analyses, Nickrent (this volume) concludes that *Arceuthobium* as a genus is markedly more variable than most plant species reported on to-date (Hamrick et al. 1979). This variability contrasts with the intra-specific uniformity in flavonoid chemistry (Crawford and Hawksworth, 1979) and morphology in this genus. At the P.G.I. locus, local variability is especially remarkable: there are 5 alleles in A.a. and 8 alleles in A.v. This locus is known to be highly variable in other plants (Gottlieb 1981). Nevertheless, this variability is unusual

considering that the total area sampled for A.v. is no more than 10 km² and for A.a. it is about 2 ha. In A.v. two locations have been sampled, and two of the alleles detected at one location in a small sample of 30 individuals have not been detected at the other (Linhart, unpublished data). The difference may be the result of limited sampling, but it does suggest that there is a good deal of genetic heterogeneity between populations. This is in keeping with the generally patchy distribution of *Arceuthobium* even within homogeneous pine forests (Hawksworth, 1978).

The genetic constitution of A.a. populations at one locus is very similar regardless of hosts (Table 1). This is not true for A.v. where there is significant difference between the population on P.p. and P.c. both at the electrophoretic (Table 2) and morphological³ levels. Considerably more detailed analyses need to be done on populations of both species to see if these preliminary results are generally applicable.

The differentiation observed in A.v. suggests that further experiments should be carried out to see if host race formation has occurred in this taxon.

Such host race formation is reported for *A. tsugense* (Smith and Wass 1976). Other studies have demonstrated the existence of intra-specific variation in mistletoes. Variation in morphology and infectivity has been documented in *Phoradendron tomentosum* (D.C.) Engelm. ex. A. Gray subsp. *tomentosum* (May 1971, 1972) and infectivity also varies in *Viscum album* L. (Paine 1950).

In addition, Hawksworth (1961) found evidence of differential infectivity of seeds of *A. vaginatum* in N. Arizona. Seeds from colonies in infected stands of ponderosa pine were used to inoculate both other trees within these infected stands and also trees from adjacent uninfected stands. Inoculations on the former were 10 times as successful as on the latter trees. Ponderosa pine, even when growing in homogeneous stands, can show very high levels of protein (Mitton et al. 1977, Linhart et al. 1981) and monoterpene (Smith, 1964) differentiation over short distances. Hawksworth's results suggest that *A. vaginatum* populations may have adapted to specific features of the biochemical phenotypes of certain stands and are then more successful at recolonizing trees of such phenotypes rather than trees of novel phenotypes. This sort of pattern has been observed in colonization of *P. ponderosa* by scale insects (Edmunds and Alstadt, 1978) and infection of specific varieties of crop plants by specific races of fungi (Barrett, 1983).

CONCLUSIONS

These preliminary results indicate that *Arceuthobium* species are amenable to analyses of genetic variability by the use of electrophoretic

methods. This is especially useful in these taxa because of their relative uniformity of morphology at the intra-specific level. In both species analyzed in some detail, given loci appear to have similar levels (i.e. high or low) of polymorphism. The rates of migration of the various allozymes at a given locus are different enough in both these species (and apparently in a third species *A. cyanocarpum*) to enable one to identify samples as belonging clearly to one or another taxon.

There are several polymorphic loci in both species analyzed. In *A. vaginatum*, at least two of these loci shows evidence of heterogeneity of allele frequencies associated with geographic location and with the host species upon which the mistletoe grow.

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The Anatomy and Morphology of the Endophytic System of *Arceuthobium* spp¹

M. Carol Alosi² and Clyde L. Calvin³

Abstract.--The part of the dwarf mistletoe plant that develops within the host plant body is termed the endophytic system. During establishment of the parasite in new areas of host stem, endophytic cells grow intrusively. After this initial invasion, the development of the endophytic system becomes attuned to the growth form of surrounding host tissues. In host secondary tissues, certain endophytic cells develop a meristem in line with the host cambium. Derivative production is coordinated with host xylem and phloem production, and endophytic cells become integrated with host ray cells to produce a chimera-like unit called an infected ray or sinker. Endophytic tissue of *Arceuthobium douglasii* is hyphal-like in primary host tissues and growth of the parasite is by cell elongation with predominately transverse divisions. Sinkers are produced when the associated host stem converts from primary to secondary growth. The relationship of *Arceuthobium* endophytic cells with host tissues reflects great tissue compatibility and careful evaluation of cytological features may be required to distinguish host from parasite cells. The organisms share a common apoplast, but symplastic continuities are doubtful.

INTRODUCTION

The part of the dwarf mistletoe plant that develops within the host has been termed the endophytic system (Thoday and Johnson 1930). There are two fundamentally different endophytic forms--depending on the species of *Arceuthobium*, the host, and perhaps the site of the original infection (Kuijt 1960). These forms produce either localized or systemic infections (Baranyay et al. 1971). The infection forms are usually easily recognized in the field since there are gross differences in the appearance of the branches.

Localized infections are contained within a limited section of the host branch and fusiform swellings, due to hypertrophy and hyperplasia of host tissues and to the presence of the

endophyte, mark the extent of the invasion of the parasite along the host stem. Aerial shoots are limited to the swollen regions and occur in random tufts. As far as is known, all *Arceuthobium* species are capable of developing localized endophytic infections on appropriate host stems (Kuijt 1960).

In contrast to the localized condition, systemic infections are produced only in the case of a few, specific combinations of *Arceuthobium* species and hosts (Kuijt 1960). Instead of being contained within a relatively limited portion of host stem, systemic infections involve entire branches of the affected host, extending into the youngest portions of the shoot, even into the buds (Thoday and Johnson 1930, Parke 1951, Kuijt 1960). Typically there is no swelling, and often infected branches are thin, elongated, and pendulous. Aerial shoots of systemic infections usually show a pattern of emergence related to the age of the host tissue (Kuijt 1960) (fig. 1). The ability to produce systemic infections is the more evolutionarily-advanced condition (Hawksworth and Wiens 1972). Most dwarf mistletoe species do not have the capacity to develop in both primary and secondary host tissues and are typically found in host secondary tissue with a limited capacity to expand vertically in the host branch.

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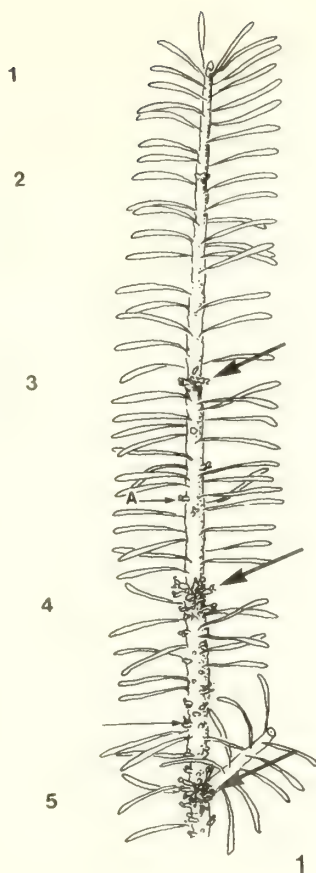


Fig. 1. A diagram of a *Pseudotsuga menziesii* shoot infected with *Arceuthobium douglasii*. The bud scale regions or segment girdles (nos. 1-5) delimit annual growth increments. Although the endophytic system occupies the entire young shoot, the aerial shoots (A) do not erupt until the host stem is 3 years old. Aerial shoots are particularly concentrated at the bud scale regions (large arrows). 1X.

Although it is well established that these two endophytic forms are stable, morphological variations in the genus *Arceuthobium*, the factors which determine form have not been fully appreciated. We believe that the major factor for endophytic form determination is whether the parasite develops within host primary or secondary tissue. Localized infections are a consequence of establishment and proliferation within host secondary tissue, while systemic infections are the result of events that allow establishment and development within host primary tissue. This simple difference has profound morphological implications.

In plant systems primary growth implies a coordinated growth of complex tissues that results in development of the vertical extension of the plant body. Secondary growth involves development of the lateral plant body, expanding the girth of the plant. The fundamental factors that coordinate the growth are not understood but we know they involve intricate processes at the subcellular level which determines cell polarities, cell division planes (Furuya 1984),

and cellulose microfibril orientation (Green 1964; Taiz 1984).

To illustrate these basic morphological forms and to show the relationship to host primary and secondary tissues we will compare the endophytic systems of *A. tsugense* and *A. occidentale*, species which form strictly localized infections, to *A. douglasii*, a species which forms diffuse infections throughout its host's primary and secondary tissues but is also capable of forming localized infections.

MATERIALS AND METHODS

For light microscope studies of localized infections of *Arceuthobium tsugense* (Rosend.) on western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and *Arceuthobium occidentale* Englem. on digger pine (*Pinus sabiniana* Dougl.) tissue was fixed in FPA (Sass 1958) dehydrated in tertiary butyl alcohol and embedded in paraffin. Twelve-micron-thick sections were stained with ferric chloride/tannic acid/lacmoid (Cheadle et al. 1953). For electron microscopy tissue was fixed in paraformaldehyde-glutaraldehyde and postfixed in osmium. Acetone-dehydrated tissue was embedded in low viscosity resin and sectioned ca. 800 angstroms.

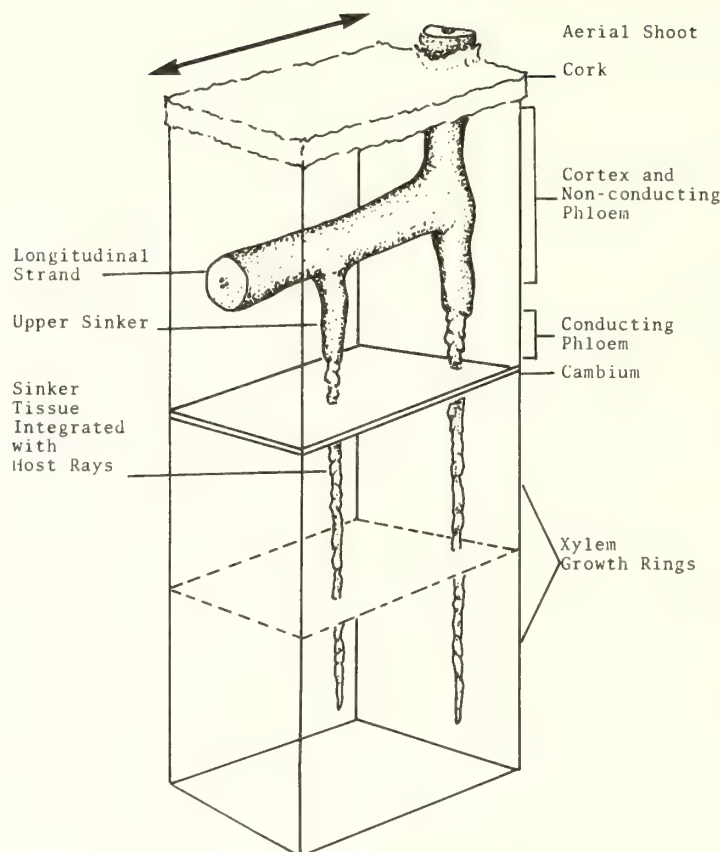
For studies of systemic infections, young stems of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were collected from branches showing dwarf mistletoe (*Arceuthobium douglasii* Englem.) systemic infection. Sections from the first and second intergirdle regions (fig. 1) were diced, fixed and embedded as described above for electron microscopy. Sections were cut at one micron and stained with aqueous 1% toluidine blue O. For low magnification work, older tissue with either localized or systemic infections was soaked in water for 1 hr and then sectioned at ca. 25 microns with a sliding microtome. Individual sections were stained with cotton blue-lactophenol, water rinsed; then stained with phloroglucinol-HCl and mounted directly in glycerol for study and photography.

OBSERVATIONS

Localized Infections

A localized infection originates from a primary haustorium at the original infection site. (The infection and establishment process is described by Dr. Knutson in these proceedings.) The primary haustorium gives rise to haustorial strands which extend longitudinally (fig. 2) and sometimes circumferentially (fig. 3) through the host cortex and outer phloem. Radially oriented growths termed "sinker" extend from the haustorial strands into the host secondary vasculature (figs. 2,3,4).

The term "sinker" was first used by Solms-Laubach in 1867 (Srivastava and Esau 1961). The usage in the literature implies reference to a discrete structure. In the green mistletoe



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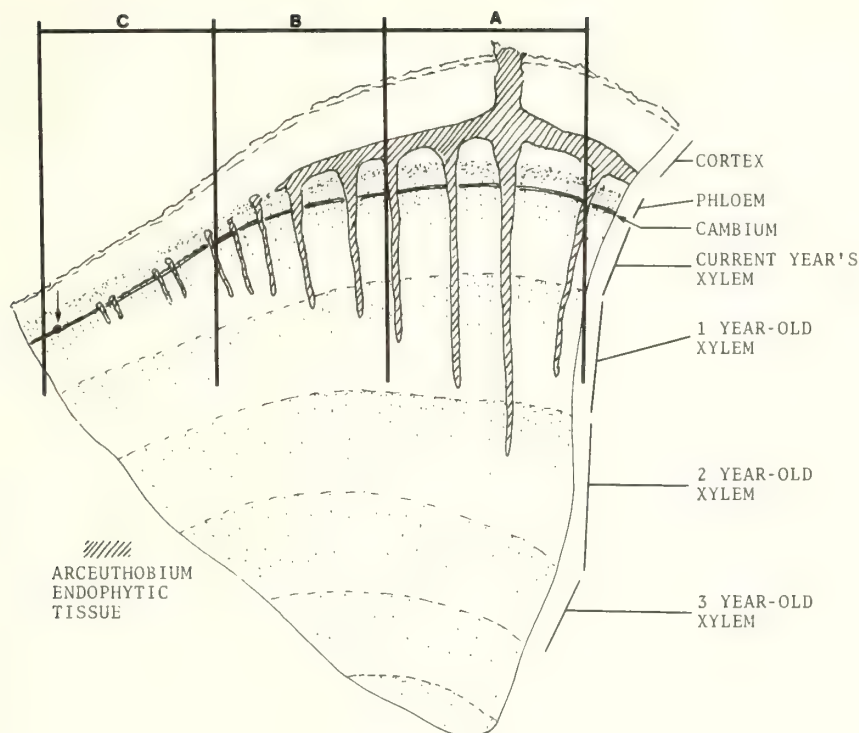
Fig. 2. A diagram of *Arceuthobium tsugense* in *Tsuga heterophylla*. The doubleheaded arrow indicates the longitudinal axis of host stem.

Phorodendron, sinkers do appear to be distinct organs of the haustorial system, as the sinkers fit like wedges into the host secondary tissue without intermingling with host cells (Calvin 1967). But, it will be seen that *Arceuthobium* sinkers lose much of their identity as individual structures during maturation of the endophytic system. We use "sinker" as a non-specific term in this report, in reference either to the radially-oriented portions of the endophytic system or to a tissue type.

Investigators differ in their interpretations of the origin and development of sinkers. Some authors report that sinkers originate as lateral protuberances from haustorial strands housed within the host bark. The radially-oriented protuberance of cells grows intrusively towards the host vascular cambium. After reaching the cambial zone the intrusive growth phase of the sinker stops (Kuijt 1960). Another version of sinker origin is that an intrusively growing portion of a longitudinal strand contacts the cambium directly, and there, on the side of the strand, sinkers are initiated

(Alosi 1980). At the contact point a series of cell divisions produces a radial file of sinker cells which becomes embedded in secondary host vasculature (fig. 3). Probably both types of sinker initiation occurs.

There are also differing views on how the radial file of sinker cells comes to be embedded in host xylem while an association with the host phloem is also maintained. Some authors believe that an intercalary meristem is formed near the host cambial zone which provides cells that subsequently become embedded in the host xylem (Thoday and Johnson 1930, Srivastava and Esau 1961). Others have suggested that the intercalary meristem is found at the "neck" of the sinker (where the sinker fuses with the longitudinal strand) (Cohen 1954, Kuijt 1960). And at least one author suggests that two meristems exist--one at the neck, the other at the host cambial zone (Parke 1951). All of these meristematic accommodations to the radial expansion of the host stem may, in fact be found among the various *Arceuthobium* species and their hosts. In tissue we have examined, we see



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Fig. 3. A diagram of *Arceuthobium occidentale* in *Pinus sabiniana*. The depth of the individual sinkers in host growth rings is indicative of the age of the infection in that precise area of the host stem. The oldest portion of the endophytic system shown is in section A, where sinkers extend into two-year-old xylem. The youngest portion is in section C, where the endophyte lies entirely within the cambial and most recently produced phloem and xylem derivatives of the host. Sinkers are initiated within the cambial zone from strand tissue that contacted the host cambium (see arrow, section C).

distinct intercalary meristems juxtaposed to the host cambium (i, fig. 5), but also the arrangement of cells in the neck of some sinkers suggests meristematic activity (arrow, fig. 5).

Sinker tissue is almost always seen in association with host rays (Thoday and Johnson 1930, Cohen 1954, Kuijt 1955 1960, Srivastava and Esau 1961). If young sinkers are originally independent of host ray tissue, new rays or existing ray derivatives are produced in relationship to the little sinker very quickly (fig. 6). The continued conversion of fusiform initials to ray initials adjacent to parasite cells results in the formation of a relatively tall, multiseriate structure consisting of radially-oriented sinker cells more or less surrounded (as seen in sectional view) by host

ray cells (figs. 4, 7).

Coordinated development of sinker tissue and ray tissue perpetuates this chimera-like morphological unit. The structure has been termed an "infected ray" by Srivastava and Esau (1961). Their terminology is appropriate since (as discussed above) the sinker no longer exists as a distinct morphological unit of the *Arceuthobium* endophyte.

Anatomy of Infected Rays

As many as five cell types are found in infected rays: host ray parenchyma, host Strasburger cells (=albuminous cells), sinker ground parenchyma, sinker xylem, and sinker sheath cells.

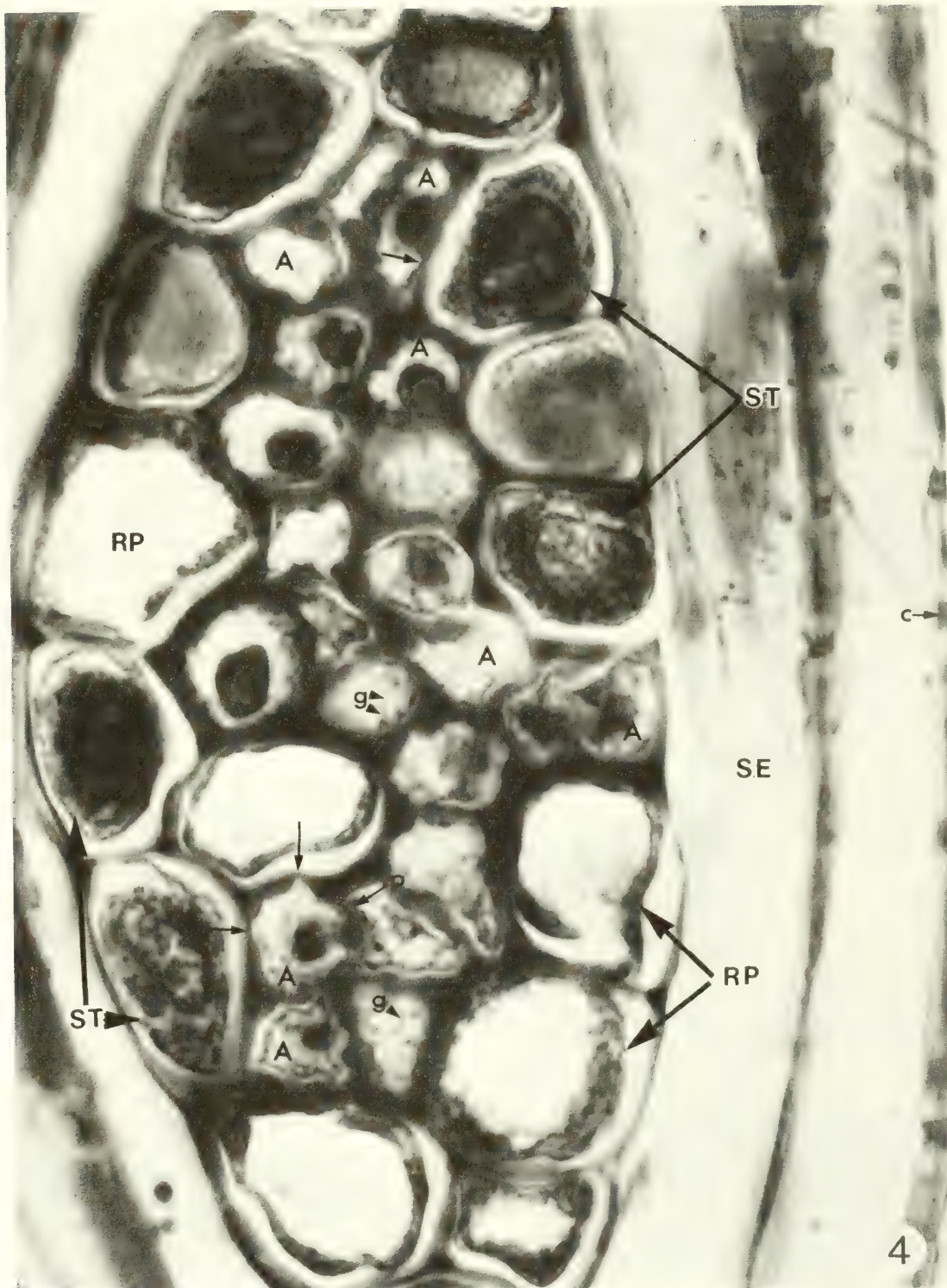


Fig. 4. An infected ray of *Tsuga heterophylla* in the region of functional sieve elements (SE). The smaller *Arceuthobium* sinker cells (A) occupy the central region; they are surrounded by host ray parenchyma (RP) and Strasburger cells (ST). Interspecific pits are at unlabelled arrows. Vacuole-like cavities (g) resulting from the removal of lipids during processing are abundant in sinker cells. c, callose; p, pit between sinker cells. 800X.

Ray Parenchyma: These host cells (RP, figs. 4,6,7) are relatively large cells with an unstained, large, central vacuole. The cytoplasm may contain starch grains and lipid bodies.

Strasburger Cells: Strasburger cells are characterized by connections with lateral sieve areas of adjacent sieve cells. They have dense granular cytoplasm, lack a large, central vacuole and are frequently more upright in orientation than the procumbent ray parenchyma (ST, figs. 4,6).

Sinker Ground Parenchyma: Sinker cells generally have a smaller diameter than host cells in the infected ray, when viewed in tangential section (A, figs. 4,6). However, sinker cells in newly-infected rays, or within the cambial zone, may be similar in size and shape to contiguous host ray cells (fig. 6). The walls of sinker ground parenchyma are usually thick, except near the cambial zone. Fresh sections stained with iodine to detect starch are negative, but lipid stains show the cells packed with large lipid bodies. In paraffin preparations, the lipids are removed and vacuole-like cavities remain (g, fig. 4). Osmium-fixed, resin-embedded material preserves lipids and the droplets are conspicuous in one-micron resin sections when phase-contrast optics are used (l, fig. 6).

Sheath Cells of the Sinker: These cells, of parasite origin, are usually found only in old, infected rays in the outer, non-conducting regions of the host phloem. The sheath cells (sh) are continuous with a layer of sheath cells around the associated longitudinal strand (fig. 5). Sheath cells of sinkers and strands have a large, central vacuole with stainable contents. The cytoplasm contains lipid cavities, and no starch.

Sinker Xylem: Strands of tracheary elements usually are found only in the larger infected rays (x. fig. 7). When xylem is present, a continuous strand may exist through the center of the sinker connecting with the xylem of an associated longitudinal strand, and inwardly with the host xylem. The parasite xylem has helical thickenings which allows extension in relationship to radial stresses. Ultimately, radial extension of surrounding tissue may destroy some of the xylary elements producing lacunae in the center of some infected rays.

Livingston et al. (these Proceedings) discusses hormonal aberrations of dwarf mistletoe infections. Therefore, the implications of abnormal hormone levels on the morphology of infected stems will not be explored here. However, we will point out that in the context of comparing localized and systemic infections, localized infections often produce striking hyperplasia and hypertrophy of xylem which appears to have a rapid onset coincident with the arrival of the sinker tissue in the vascular cambium (fig. 15). Figure 2 illustrates that the

abnormal xylem production is not transmitted evenly around the vascular cylinder, but is localized within a short distance from the parasite sinker tissue. When a localized infection does not circumscribe the host stem, the abnormally wide growth rings will be found only where the sinker tissue is. Cambial cells only a few mm away may produce normal derivative numbers. In old infections, perhaps in response to decline, the growth rings become smaller in width.

Function of Sinkers.

Because of juxtaposition of host xylem and phloem with sinkers, the latter are considered to be important in parasite nutrient acquisition. Direct apoplastic continuity through interspecific xylem contacts and cellulose wall free space provides pathways for water and mineral extraction. The parasite also obtains substantial amounts of host-originating photosynthate (Hull and Leonard 1964) and investigators have for many years thought that transfer of organics occurs in the region where the sinkers cross host phloem (Pierce 1905, Weir 1916, Gill 1935, Leonard and Hull 1965). How could these normally symplastically held nutrients be acquired? Direct contact with the host sieve cells is usually found only in small sinkers (figs. 6,7). Sinkers seem more intimately associated with host ray cells and pits occur in the cell walls between the two organisms (arrows, figs. 4). When examined by the electron microscope we find that these pits often have half plasmodesmata (*sensu* Burgess 1972) extending from the host to the parasite. The half plasmodesmata end blindly at the middle lamella (fig. 8). Thus, pits are not indicative of interspecific symplastic continuity via plasmodesmatal connections. Because the organisms are symplastically isolated from each other, we must conclude that in dwarf mistletoe infected stems, the soluble organic nutrients, which are normally held within the symplast of the host, are leaked into the common apoplast of the two organisms. Eventually these nutrients are absorbed into the parasite symplast before being transported into the aerial shoots. We know this, because tracer studies have shown that when the bases of aerial shoots are steam killed, host-fixed carbon compounds are not transported into the shoots, although transpiration continues (Hull and Leonard 1964).

Systemic Infections.

Growth in primary tissues--the primary endophytic form.

Kuijt (1960) reported the presence of *A. douglasii* endophytic tissue in Douglas-fir dormant buds. He found that the distribution of parasite tissue in the buds is related to the host procambial strands which develop in relationship to leaf primordia and to a procambial plexus at the base of the bud. When budbreak occurs, cell division and elongation

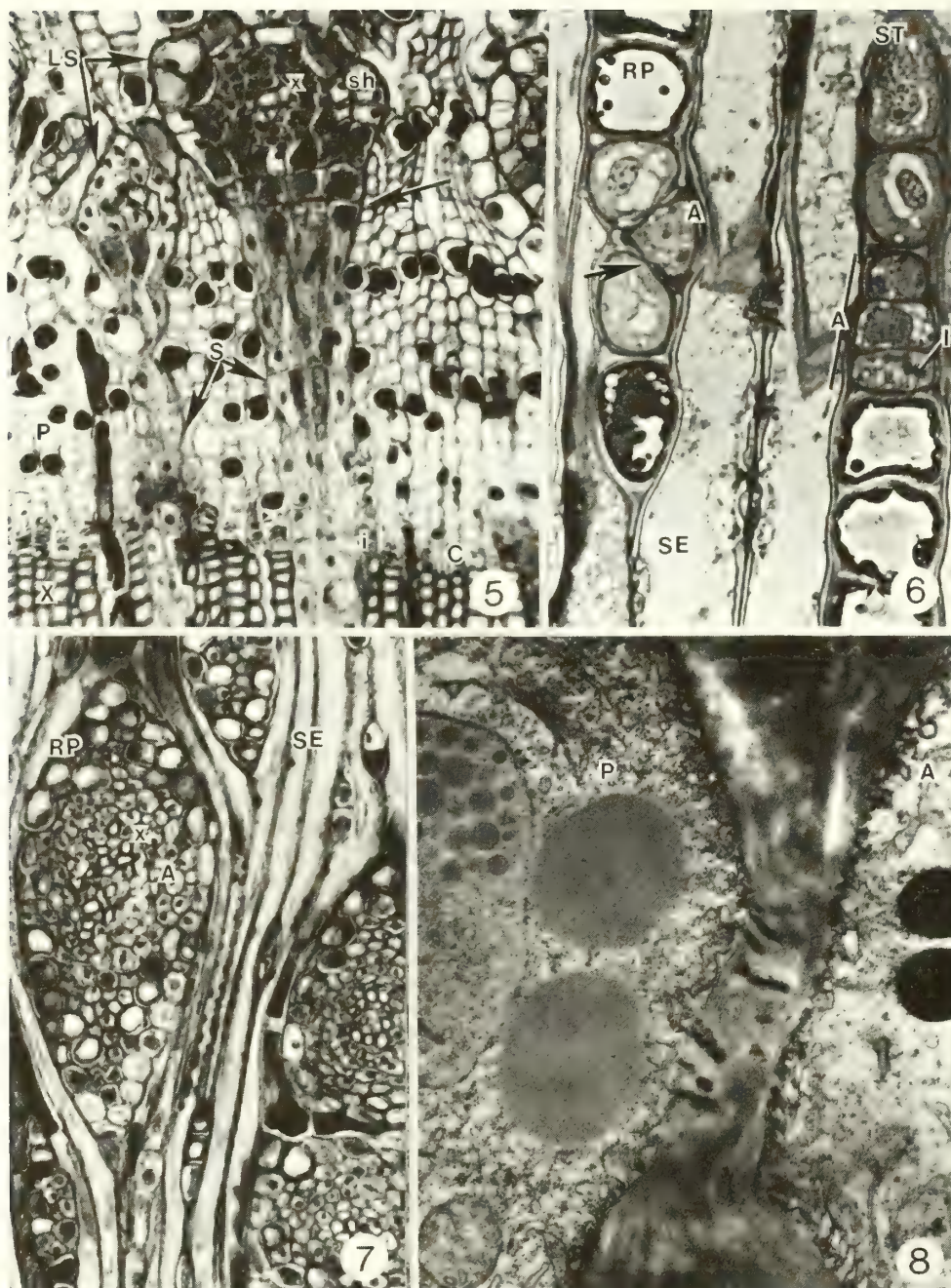


Fig. 5-8. Fig. 5--Infected *Tsuga heterophylla* tissue. Cross section. Longitudinal haustorial strands (LS), one with a central core of xylem (x), connect with sinkers (S). Sinker sheath cells are confluent with the longitudinal strand sheath cells (sh) where a neck meristem (arrow) may adjust the sinker to the radial expansion of the host stem. At the region of the host cambium (C) sinker initials (i) produce derivatives in coordination with xylem (X) and phloem (P) production. 110X. Fig. 6--Young infected rays of *Tsuga heterophylla* in the recently differentiated phloem. Sinker cells (A) and host ray cells have pit connections (arrow). Resin-embedded tissue, phase contrast. 1, lipid droplet; RP, ray parenchyma; ST, Strasburger cell; SE, sieve element. 500X. Fig. 7--Old infected rays of *Tsuga heterophylla* in mature phloem. Sinker tissue (A) is surrounded by host ray cells (RP). Sinker xylem (x) occupies the center of the infected rays. 100X. Fig. 8--Electron micrograph showing a typical pit between *Arceuthobium occidentale* (A) and a *Pinus sabiniana* ray cell (P). The cell wall interface of host and parasite is fused and very thin at the pit. Half plasmodesmata occur on the host side. 30,000X

develops the bud acropetally (Allen 1945) and the associated endophytic tissue develops simultaneously. Our investigation of A. douglasii systemic infections begins with studies of one-year-old stem segments, after the elongating bud stage, when primary growth is well established but before secondary growth begins (fig. 3). We term the parasite tissue associated with primary host tissue the primary endophytic form of systemic infections.

Because of the very close developmental, relationship between host and parasite and the complex assortment of cells in the young shoot, identification of Arceuthobium cells is not always obvious (figs. 9,10). Two cytological details were used to identify parasite cells--nuclear structure and lipid storage bodies.

Arceuthobium has chromocentric nuclei, while Douglas-fir has reticulate nuclear structure (re: Lafontaine 1974). The chromocentric nuclei of A. douglasii have a delicate meshwork of euchromatin throughout the nucleoplasm with dense, heterochromatin masses associated with the nuclear envelope or with the single, sometimes enlarged and vacuolated nucleolus (CN, fig. 11). The reticulate nuclei of Douglas-fir cells (RN) have a conspicuous reticulum of chromatin and lack of heterochromatin masses in the interphase condition (compare RN and CN in figs. 10,11).

The second method of identification is based on the appearance of lipid bodies and is most obvious with phase contrast optics. Arceuthobium cells store lipids in large lipid droplets (I, fig. 11), while Douglas-fir cells store lipids in small spherosomes (s, fig. 11).

The primary endophytic tissue of A. douglasii present within the relatively mature primary host shoot is composed of a complex of mainly uniseriate, hyphal-like strands. The concentration of parasite tissue is greatest in the position of the former procambial plexus, at the girdle-bud scale region. Both host and parasite cells are short, have dense protoplasm, and appear irregularly arranged in this region.

Longitudinal sections of infected year-old stems from the intergirdle region are seen in figs. 9 and 10. The epidermis (e) encases the large, loosely-packed cortical cells (C). Internal to the cortical cells are extremely long, empty-appearing ducts (d) which are lined on their centripetal side by living duct cells (dc). The primary vascular tissue lies to the inside of the duct cells and consists of long, primary sieve cells (SE), shorter Strasburger cells (ST), storage parenchyma with ergastic vacuole contents (st), procambial tissue (or undifferentiated derivatives, pr), and xylem (x). In the center of the young stem is the pith (not shown).

In the intergirdle region some parasite cells are found in neat, longitudinal files within the host primary phloem (fig. 13). It is likely that this tissue is derived from tissue originally associated with the host's procambial strands and it elongated simultaneously with host procambial tissue while undergoing regular transverse divisions. During elongation of the Douglas-fir shoot, the procambium is enlarged by lateral addition to existing procambial strands. Arceuthobium douglasii appears to associate with this additional vasculature by hyphal-like, tortuous extension of endophytic tissue through the cortex (A, fig. 9, 13) with subsequent deflection towards the cambial cylinder and intrusive growth into the host phloem and procambium (fig. 12).

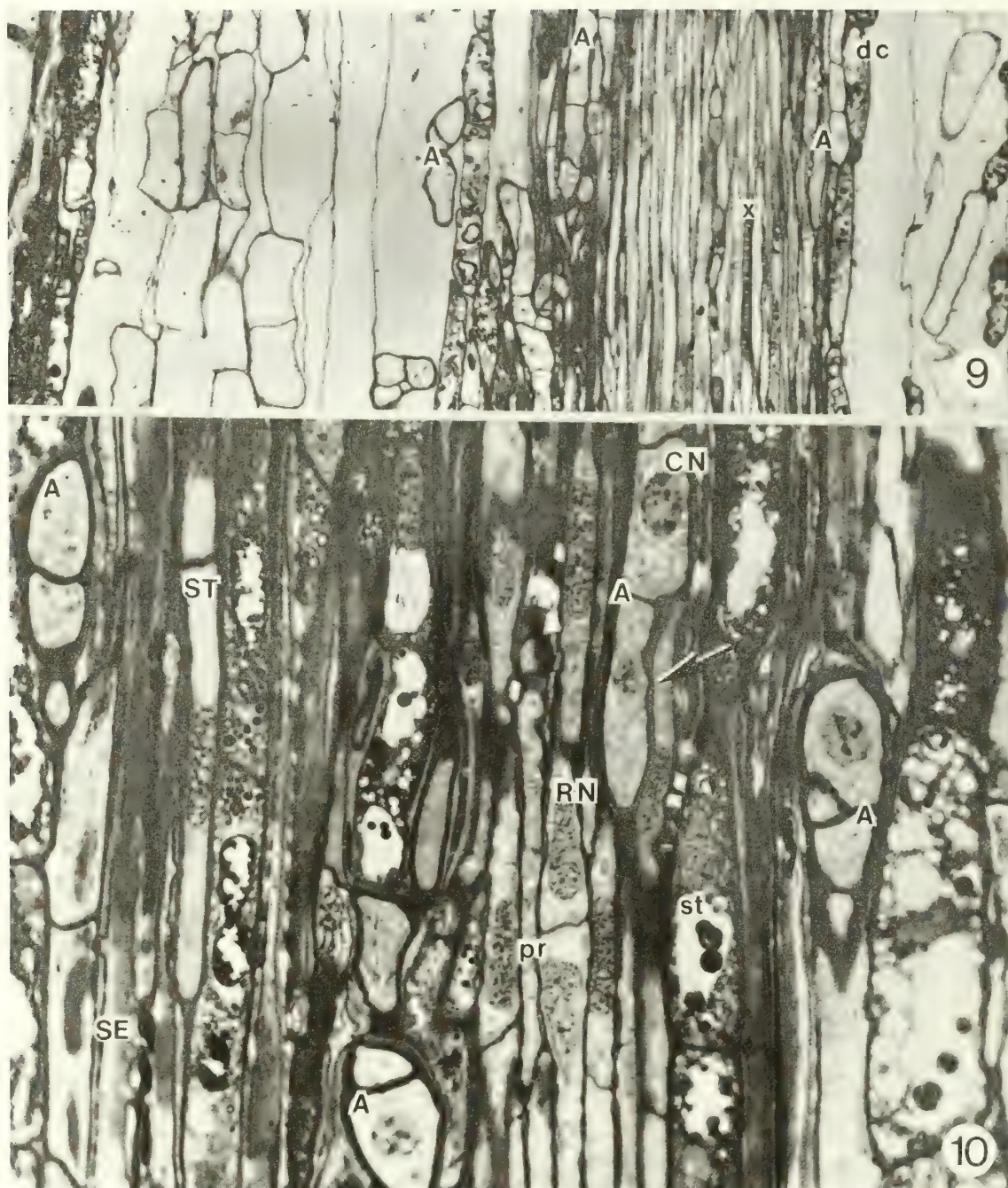
In contrast to the arrangement of cells in localized infection, no sinkers or multiseriate haustorial strands develop in the primary endophytic form of A. douglasii. Only the inner cortex, the phloem, and the procambium are invaded. The parasite cells of primary endophytic tissue all appear to be the same cell type--no specialized cells differentiate in relationship to host phloem and no tracheary elements form. However, as in the infected rays of secondary tissue, pits are frequently found between parasite and juxtaposed host cells of the primary plant body (unlabelled arrow, figs. 10,11).

Growth in secondary tissues--the secondary endophytic form.

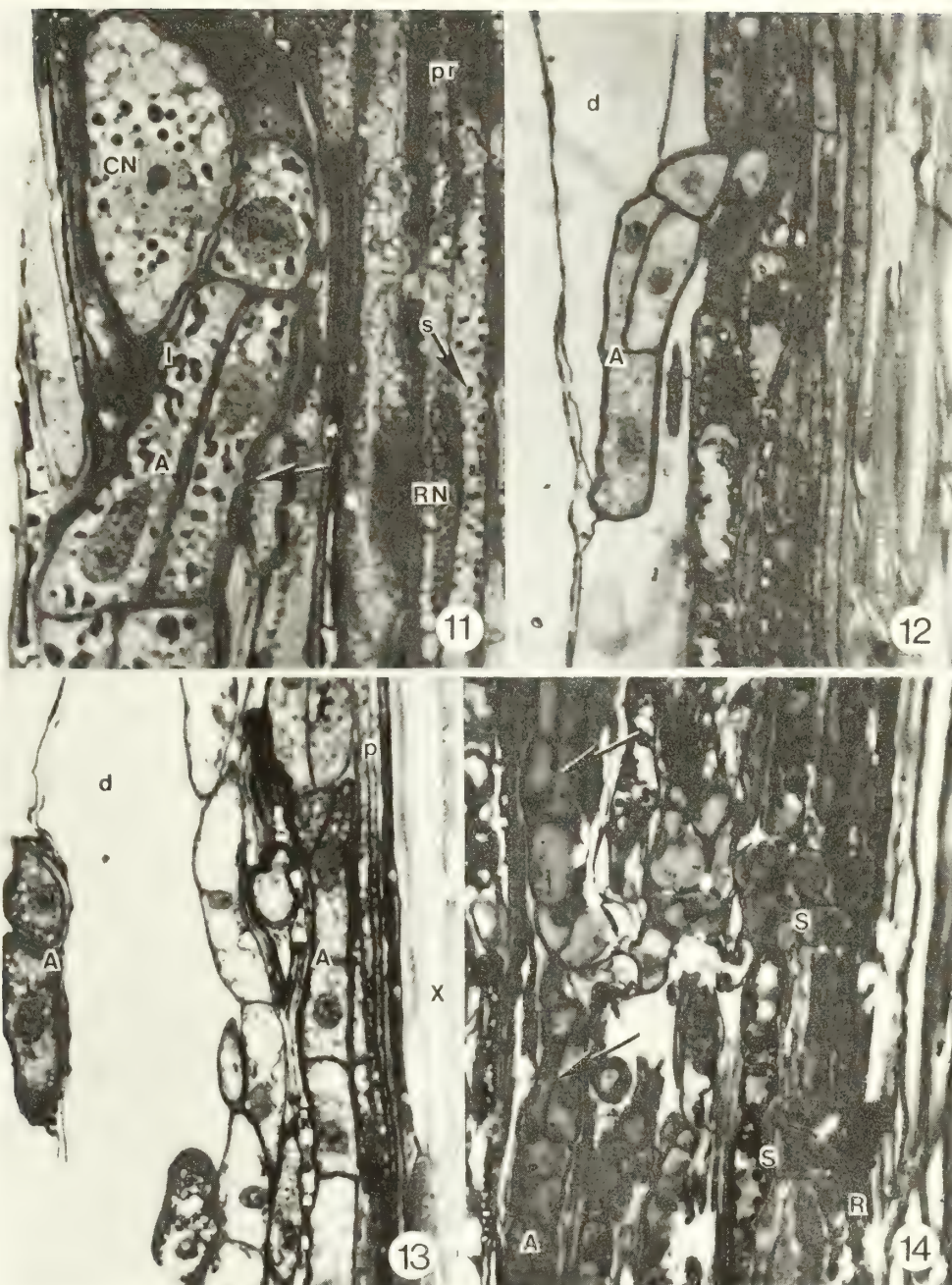
The beginning of secondary growth is marked by formation of the vascular cambium and a shift from axillary development to lateral growth and differentiation. The predominately uniseriate strands of A. douglasii established during development in the host primary shoot, begin the transition to the more complex, multiseriate, longitudinal strands of the secondary endophytic form by ceasing elongation, expanding radially, and undergoing periclinal division (unlabelled arrow, fig. 14).

The host vascular cambium appears to have a growth polarizing effect on endophytic tissue. Apical cells of hyphal-like strands respond by intrusively growing towards the cambium. Other cells, in intercalary positions of hyphal-like strands of the primary endophytic system, develop outgrowths that extend toward the vascular cambium (S, fig. 14). Growth is intrusive among medullary rays, declining tiers of secondary phloem derivatives, and newly formed ray cells (R, fig. 14). These radially oriented strands of Arceuthobium cells will become the sinkers of the secondary endophytic system within the secondary host tissue.

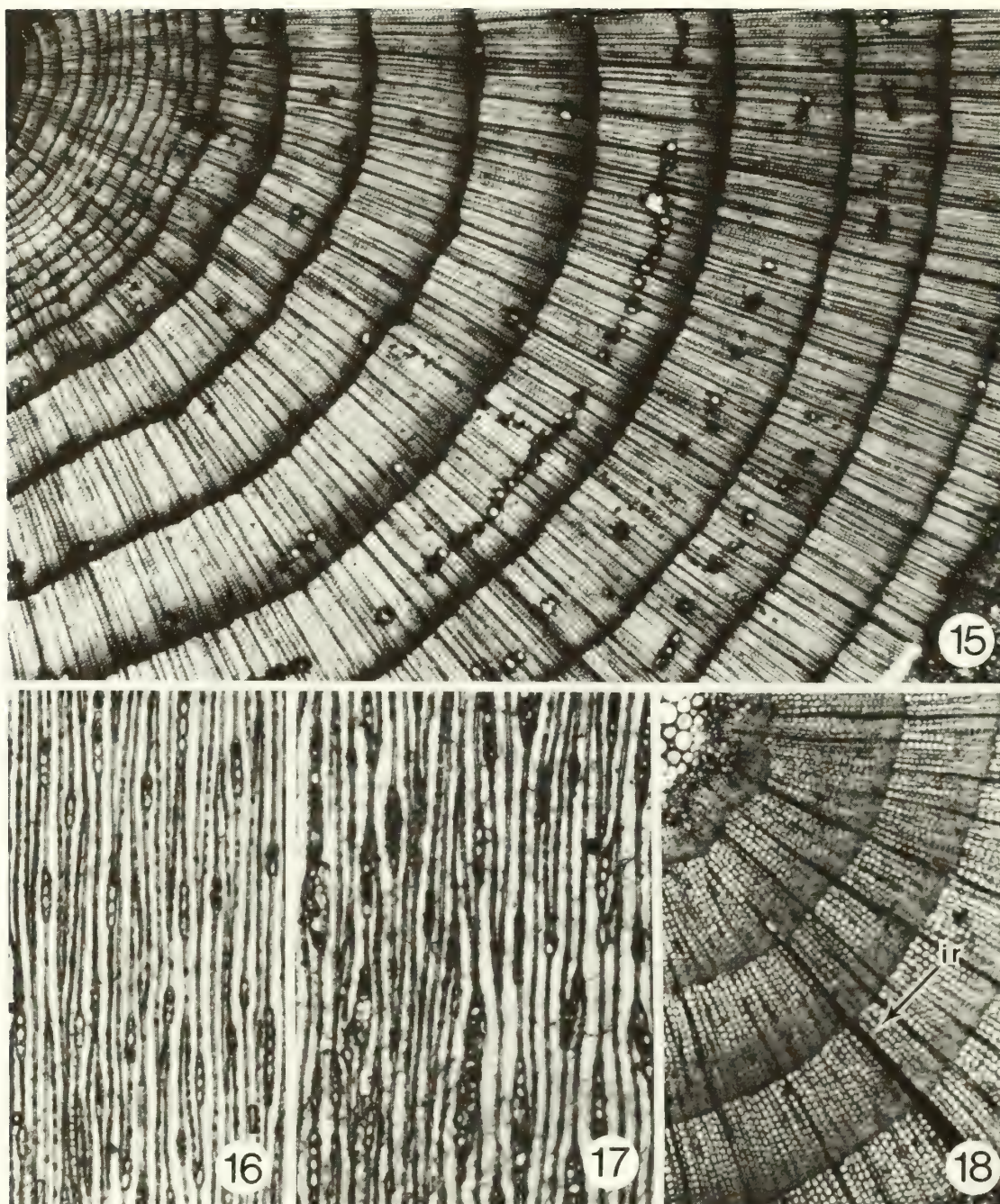
The basic structure of A. douglasii endophytic tissue of systemic infections in secondary vasculature is the same as that established in localized infections, i.e., haustorial strands, and sinkers. As in localized



Figs. 9 and 10. Tangential section infected primary shoot of *Pseudostuga menziesii*. Fig. 9--Strands of the primary endophytic system of *Arceuthobium douglasii* (A) are found in the inner cortex (C), primary phloem (p); d, duct; e, epidermis; pr, procambial tissue. 50X. Fig. 10--Hyphae of the primary endophyte (A) is integrated into the primary phloem of the host. The reticulate nuclei of the host (RN) is distinct from the chromocentric nuclei of the parasite (CN). SE, sieve element; st, storage parenchyma; ST, Strasburger cell. 200X.



Figs. 11-14. *Arceuthobium douglasii* in Douglas-fir primary tissue. Longitudinal sections; 1 micron thick. Fig. 11--Parasite cells (A) with large lipid droplets (l) and characteristic chromocentric nuclei (CN) are associated with host phloem and procambial tissue (pr) which have small spherosomes (s) and reticulate nuclei (RN). 500X. Fig. 12--A hyphae of *Arceuthobium* tissue (A) within the ducts (d) of the host shoot appears to be invading host vascular tissue by intrusive growth. 170X. Fig. 13--Hyphal strands of the parasite (A) are longitudinally oriented within the primary phloem of the host (p) and do not extend into the xylem (X). Hyphal strands also grow intrusively between ducts (d). 150X. Fig. 14--The transition of the primary endophytic form to the secondary endophytic form seen in radial section. Radial expansion of hyphal strand (A) and periclinal division (arrow) of cells marks the first stage in conversion of the hyphal strand to the multi-seriate haustorial strands of the secondary endophytic form. Sinkers, found only in the secondary endophyte, form from radially-oriented protrusions (S) which grow intrusively through newly formed rays (R). 175X.



Figs. 15-18. Infected and uninfected wood of *Pseudotsuga menziesii*.
 Fig. 15--Cross section. Stem with localized infection of *Arceuthobium douglasii*. The outer 9 rings show hypertrophy which is characteristic of localized infections. The smaller, inner rings were produced prior to infection. 20X. Fig. 16--Tangential section. An inner, uninfected growth ring from tissue shown in Fig. 15. Small, normal, uniseriate rays are found. 50X. Fig. 17--Tangential section through an outer, hypertrophied ring from tissue shown in Fig. 15. Rays are abnormally wide due to the presence of *Arceuthobium* cells within the rays. 50X. Fig. 18.--Cross section of stem having systemic infection symptoms. Uniform growth rings are present despite the presence of the parasite. Infected rays are narrow except those that formed from medullary rays (ir). 35X.

infections the secondary endophytic form may have ground tissue, xylem, and sheath cells (Parke 1951).

There are no localized swellings in secondary host tissue with systemic infections because the secondary endophytic form develops from the pre-existing primary endophytic system, and the conversion to the secondary endophytic form occurs more or less simultaneously throughout the entire stem segment. There is apparently less anomalous wood structure in systemic infections, perhaps as a consequence of the continual association of parasite and host tissues. Growth rings are of a consistent size and traumatic resin ducts, present in localized infections, are not seen in the wood of *A. douglasii* systemic infections (compare figs. 15 and 18). The pendulous growth habit of systemically-infected Douglas fir branches is a consequence of abnormal elongation during primary growth.

CONCLUSION

The dwarf mistletoes are remarkably attuned to host growth, whether primary or secondary. Because of the parasite's sensitivity to the developmental processes of its host, *Arceuthobium* species that form systemic infections keep pace with the longitudinal growth of the host stem by hyphal-like extensions of a diffuse, primary endophytic system. Later, in areas where the host's primary growth stops and conversion to secondary growth occurs, the associated dwarf mistletoe tissue morphologically adjusts in accommodation to the new host growth form. Parasite growth in secondary host tissues in all *Arceuthobium* species, whether in systemic or localized infections, is characterized by the development of radially oriented sinkers. By coordinating derivative production with host cambial activity, sinkers become embedded in host xylem and remain intimately associated with the annual phloem increment. Sinkers lose their identity as individual morphological structures very quickly after their initiation. They become integrated into rays to form the chimera-like infected rays.

The function of sinkers is presumed to be both nutrient absorption and facilitation of nutrient transport out of the host vasculature. How this process occurs is not clear since the dwarf mistletoes have no phloem even in the aerial shoots. (Relic sieve elements have been discovered by Calvin (in press) which are associated with fruit in a primitive *Arceuthobium* species). The total absence of phloem is an anatomical feature shared by few other vascular plants and the loss of this fundamentally important tissue is a physiological adaptation which we do not understand.

Studies on the morphology of the encophytic systems of *Arceuthobium* have illucidated the

highly developed accomodation of the parasite to the host anatomy and physiology. This is demonstrated most strikingly in systemic infections where both the primary and secondary host tissue is parasitized and growth is closely coordinated. Anatomical studies have shown that interspecific symplastic union does not occur. Furthermore, interspecific xylary connections with a continuous haustorial xylary system is not necessarily established throughout the endophytic system. (In fact, in the primary endophytic system of *A. douglasii* no xylem is differentiated and contact with host xylem does not generally occur). The physiological implication of these morphological facts is that the cellulosic cell wall portion of the free space continuum which joins host and parasite is in all probability the major conduit for interspecific nutrient flow, as well as being important in water conduction. We know, however, that eventually living parasite cells are involved in the transport of organic nutrients into the aerial shoots (Hull and Leonard 1964), but the precise route and rate of transport is unknown.

These facts may be helpful in developing chemical control methods for dwarf mistletoes. In order to select systemic pesticides for specific needs, it is helpful to understand both the translocation characteristics of a compound, and whether the target pest is associated with the host's symplast, apoplast, or both. The apparent importance of the free space continuity in dwarf mistletoe/host nutritional relationships might well be exploited in development of control measures.

It has been twenty years since Leonard and Hull published their pioneering tracer experiments in host/mistletoe nutritional relations. Unfortunately, very little similar work has been done since. In the future one hopes that sugar transport rates into aerial shoots will be determined. This information is essential for further understanding of transport phenomenon in aphloic tissue such as the dwarf mistletoes. In addition, tracer work which allows microautoradiography of diffusible substances will be most valuable, allowing visualization of transport paths between host and parasite and within the dwarf mistletoe endophytic system and aerial shoot tissue. Such precise knowledge of interspecific nutrient transport will be fundamental to research associated with effects of exogenous substances on the mortality of the parasite.

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Altered Concentrations of Absciscic Acid, Indole-3-Acetic Acid, and Zeatin Riboside associated with Eastern Dwarf Mistletoe Infections on Black Spruce¹

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Abstract.--Noninfected stem segments of black spruce (*Picea mariana*), and stem tissue infected with eastern dwarf mistletoe (*Arceuthobium pusillum*) were analyzed monthly from April to October, 1982, for absciscic acid (ABA), indole-3-acetic acid (IAA), zeatin, and zeatin riboside. High performance liquid chromatography was used to purify all plant extracts and to ascertain concentrations of IAA, zeatin, and zeatin riboside. ABA levels were analyzed using gas chromatography. Zeatin was not detected while zeatin riboside was detected only in samples collected in April-June. Concentrations of zeatin riboside (up to 65 ng/g fresh wt) were higher in infected tissue in 15 of 18 comparisons. IAA concentrations (28-479 ng/g fresh wt) were higher in 15 of 16 comparisons from April and May samplings. Impurities in the samples prevented adequate analysis of IAA from June to October. ABA levels (37-1546 ng/g fresh wt) were consistently lower in infected tissue ($P(T) < 0.1$) throughout the sample period. Alterations in plant growth substances are apparent in successful infections of dwarf mistletoe.

INTRODUCTION

Dwarf mistletoes (*Arceuthobium* spp.) can alter normal growth of conifers as indicated by (1) proliferation and elongation of tree shoots (Tinnin and Knutson 1980), (2) swelling of the infected stem tissue, and (3) reduction in tree growth that may lead to death (Hawksworth 1978).

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The reduction in growth occurs because dwarf mistletoe does not supply all of the photosynthetic assimilates it uses (Miller and Tocher 1975) and obtains assimilates from its host (Hull and Leonard 1964), i.e. it acts as an assimilate sink. The parasite is thought to induce these changes in its host by altering the balance of plant growth substances in the tree tissue, particularly cytokinins (Knutson 1979). Studies (Paguet 1979, Schaffer et al. 1983) have shown higher concentrations of cytokinins (zeatin and zeatin riboside) or cytokinin-like activity in tissue infected with dwarf mistletoe than noninfected tissue.

Other plant growth substances are known to affect source-sink relations in plants (Wareing and Patrick 1975) but have not been analyzed for dwarf mistletoe infections. A better understanding of how dwarf mistletoe infections affect other plant growth substances besides cytokinins is necessary to ascertain how this parasitic plant is able to obtain assimilates from its host. This study compared the amounts of indole-3-acetic acid (IAA), absciscic acid (ABA) as well as zeatin and zeatin riboside associated in black spruce (*Picea mariana* (Mill.) B.S.P.) tissue infected by eastern dwarf mistletoe (*A. pusillum* Pk.) vs. noninfected tissue.

MATERIALS AND METHODS

Tree Material.--Black spruce tissue infected with eastern dwarf mistletoe was obtained from an uneven aged stand (tree age up to 120 yr) on the Fond du Lac State Forest, Carlton Co., MN. Tissue for plant growth substance analysis was collected during the third week of each month from April through October, 1982. Trees were selected by establishing a 2 m wide transect in a random direction through the stand. From the trees whose stems were within the transect and whose crowns were dominant or codominant in the overstory, four trees with male infections of eastern dwarf mistletoe and four trees with female infections were selected at random. A new tree sample was obtained for each month of tissue collection. The branch with the dwarf mistletoe infection was tagged as well as a noninfected branch originating from the same node on the tree stem. Branch segments that had formed one and three years previously were cut from the two branches and placed on dry ice. Sampling occurred during mid-day. Needles, buds, and new growth were removed, the segments were cut into 1-5 mm pieces, and the tissue was immediately frozen until extraction.

Extraction.--Extraction took place in a cold room at 1 to 2 C. Within 24 hr of collection, one gram of the sliced tissue segments were placed in 50 ml of 80% methanol containing 10 mg/l butylated hydroxy-toluene (Calbiochem, LaJolla, CA) and homogenized with a Polytron homogenizer (Brinkman Instruments) for 5 min at 1 G. Prior to homogenizing, ca. 5,000 dpm of [14 C]IAA (52 mCi/mmol, Amersham) and (\pm)[14 C]ABA (17.9 mCi/mmol, Amersham) were added to each sample to quantify the recovery efficiency. After homogenizing, the samples were placed overnight on a shaker at 1 C. On the following day the samples were filtered, reduced to aqueous phase *in vacuo* at 30 C, frozen and thawed, and then centrifuged at 15,000 g. The supernatants were then reduced to dryness *in vacuo* at 30 C and stored at -20 C.

Purification.--Samples were purified using high performance liquid chromatography (HPLC) as described by Schussler et al. (1984) and Hoover (1982). Samples were resuspended in 4 ml water, filtered, and injected into a 2-column HPLC system consisting of PRP-1 (a porous polystyrene gel) and RSiL. The mobile phase for the first column was a pH/ethanol gradient and for the second column an ethanol gradient. Based on elution times for standards, separate fractions were collected for the cytokinins, IAA, and ABA. Additional purification of the cytokinins and IAA was done with a 1-column HPLC using Nucleosil and 0.1 N acetic acid/acetonitrile mobile phase. Zeatin and zeatin riboside were separated at this time.

Quantification.--Zeatin and zeatin riboside were quantified using HPLC with a cation exchange column and two UV detectors connected in series monitoring at 254 nm and 210 nm (Hoover 1982). IAA was quantified using an anion exchange column

and two different detectors (fluorescence and oxidative amperometric) connected in series (Hein et al. 1984). Amounts of the compounds were estimated by comparing peak heights of the samples to those of an external standard curve. Ratios of peak heights as measured by the two different detectors were calculated for each sample and were compared to the mean ratio of the standards. If the ratio of a sample was more than 2 standard deviations from the mean ratio of the standards, the peak of the sample was considered impure. After HPLC analysis, the IAA fractions were analyzed for radioactivity using liquid scintillation spectrometry to calculate the loss of [14 C]IAA during purification and quantification.

ABA fractions were methylated and then quantified using gas liquid chromatography with an electron capture detector (Schussler et al. 1984). The methylated samples and standards of ABA were brought up in 500 μ l of ethyl acetate containing the ethyl ester of ABA as an internal standard. One μ l was injected (1:10 split ratio) into the capillary column. Quantification was based on the ratio of the methyl ester peak height to the ethyl ester peak height. The remaining volume in the ABA samples was analyzed for radioactivity of (\pm)[14 C]ABA.

Authentication of zeatin riboside and IAA was accomplished using gas chromatography-mass spectrometry (GC-MS). Mass spectra were obtained using a KRATOS MS-25 GC-MS operating at an ionization potential of 70 eV with a DS-55 data system. Cytokinins were derivitized at 55 C for 0.5 h with N,O-bis (trimethylsilyl)trifluoroacetamide-trimethylchlorosilane (99:1, 5 μ l; Regis Chemical Co., Morton Grove, IL) with 5 μ l of pyridine as solvent. The GC-MS ran with a temperature programmed from 160-280 C at 40 C/min, flow rate 2 ml/min. A 10 m methyl silicone fused silica column (0.53 mm dia.) (Hewlett Packard) was used. IAA samples were derivitized with 6 μ l BSFTA (Regis Chemical Co., Morton Grove, IL) for 0.25 h at 50 C and were run on the GC-MS with a temperature programmed from 60-240 C at 40 C/min. Samples were run on a 25 m cross-linked 5% phenyl methyl silicone fused silica column (0.3 mm dia.) (Hewlett Packard).

To avoid the assumptions of normal distribution and equal variances, nonparametric statistical tests were used as described by Conover (1980). To reduce the variation in concentrations of plant growth substances due to sampling different trees, observations made on the same tree were paired for statistical analysis.

RESULTS

Zeatin and Zeatin Riboside.--No peaks occurred in the fraction that eluted with the zeatin standard during HPLC analysis, and therefore this compound was not detected in any of our samples. Small amounts of zeatin riboside were detected only in the first three sample

months. During analysis, the only peaks that appeared in the fraction which corresponded with the elution time of the zeatin riboside standard were judged to be pure zeatin riboside. GC-MS of the samples showed mass spectra characteristic of TMS-zeatin riboside (Dauphin et al. 1977). Nondetectable amounts of zeatin and zeatin riboside were 5 ng/g fresh wt or less. Losses during purification and analysis were not computed.

In the April samples, amounts of zeatin riboside were larger from infected tissue than from noninfected tissue in 5 of 6 pairings (one yr old branch segments: 24,15; 14,<5; 10,9; 25,17; 10,18 ng/g fresh wt. Three yr old branch segments: 8,<5 ng/g fresh wt). In the May samples, zeatin riboside values were higher in 4 of 6 pairings (one yr old branch segments: 65,<5; 11,<5; 11,<5 ng/g fresh wt. Three yr old branch segments: <5,39; 12,<5; <5,12 ng/g fresh wt.). In the June samples, amounts were larger in 6 of 6 pairings (one yr old branch segments: 16,<5; 14,<5; 53,<5; 13,<5; 13,<5 ng/g fresh wt. Three yr old branch segments: 10,<5 ng/g fresh wt.).

IAA.--IAA was detected in our samples throughout the growing season (fig. 1), but most samples collected after May were judged to have impure IAA peaks during HPLC analysis and were excluded from further consideration. GC-MS of the samples showed mass spectra characteristic of bis-TMS-IAA (McDougall and Hillman 1978). The amounts of IAA detected in our samples were corrected for losses of [14 C]IAA which averaged 35% recovery for April, 30% for May, and 17% for the remaining months. In April, all ten possible pairings of infected and noninfected branch segments had higher concentrations of IAA in the infected tissue. Five out of the possible six pairs in May had larger amounts of IAA associated with dwarf mistletoe infection. For the time period after May, only three out of the possible nine pairs had higher concentrations of IAA in the infected tissue. Because of the large number of missing values, statistical tests were not completed on this data set.

ABA.--Compared to the other plant growth substances analyzed, large amounts of ABA were detected in the samples (fig. 2). Amounts of ABA were corrected for the losses of [14 C]ABA, and the recoveries averaged 66%, 71%, 77%, 61%, 72%, 73%, and 69% for the respective sampling months of April through October.

For each grouping of branch segments, ABA concentrations for male and female infections did not differ (Mann-Whitney test, $P(T)>0.1$) except for one yr old branch segments in October ($P(T)=0.05$). This difference was probably due to the variation of ABA levels observed for this month. Therefore, branch segments from male and female infections of eastern dwarf mistletoe were pooled for the remaining analyses.

Additional statistical analyses were done using differences of paired observations; the ABA concentration of the infected branch segment was

subtracted from the ABA concentration of the corresponding noninfected branch segment on the same tree. The size of the differences between infected and noninfected tissue did not differ between one yr old branch segments and three yr old branch segments for April, July, and October (Wilcoxon Signed Ranks Test, $P(T)>0.1$), but differences in the concentrations of ABA between infected and noninfected tissue were larger in one yr old branch segments for the other months ($P(T)<0.05$). Therefore, additional statistical tests were calculated separately for the two different branch segments. The size of the differences in ABA concentrations between infected and noninfected tissue were significantly different between months (Kruskal-Wallis Test, $P(X)<0.05$ for one yr old branch segments and $0.05<P(X)<0.10$ for three yr old branch segments). Therefore, values for each month were not pooled, and calculations for the significance of the differences between infected and noninfected tissue were derived for each branch segment within each month. These differences in ABA concentrations between infected and noninfected tissue were significant for each combination of month and branch segment (Wilcoxon Signed Ranks Test, $0.05<P(T)<0.1$ for three yr old branch segments in October, $P(T)<0.05$ for the remaining combinations).

Differences in ABA concentrations between one yr old branch segments and three yr old branch segments for infected tissue were significant only in April (Wilcoxon Signed Rank Test, $P(T)<0.05$) and in July ($0.05<P(T)<0.1$). In contrast, ABA concentrations were significantly larger ($P(T)<0.05$) in one yr old branch segments than the three yr old branch segments for noninfected tissue for each month except April and October ($P(T)>0.1$).

DISCUSSION

Zeatin and Zeatin Riboside.--There was more zeatin riboside in spruce tissue infected with eastern dwarf mistletoe than noninfected tissue. This confirms previous observations of increased cytokinin activity associated with dwarf mistletoe infections (Paquet 1979, Schaffer et al. 1983). Zeatin was not detected in any samples but still may be present in black spruce tissue. Paquet (1979) found zeatin in stem tissue of Douglas-fir (*Pseudotsuga menziesii*) infected with *A. douglasii* and in stem tissue of western hemlock (*Tsuga heterophylla*) infected with *A. tsugense*. Zeatin was not detected in noninfected tissue of these two conifers and was detected less frequently than zeatin riboside in the infected tissues. Zeatin riboside was rarely detected in our samples (22 of a possible 224). Twenty of the 22 concentrations were below 25 ng/g fresh wt. Apparently the amounts of zeatin riboside extracted from conifer tissue are small as observed in our study with black spruce and in the study of Little et al. (1979) with balsam fir (*Abies balsamea*, 5 ng/g fresh wt for the cambial region). Also, zeatin riboside was most prevalent

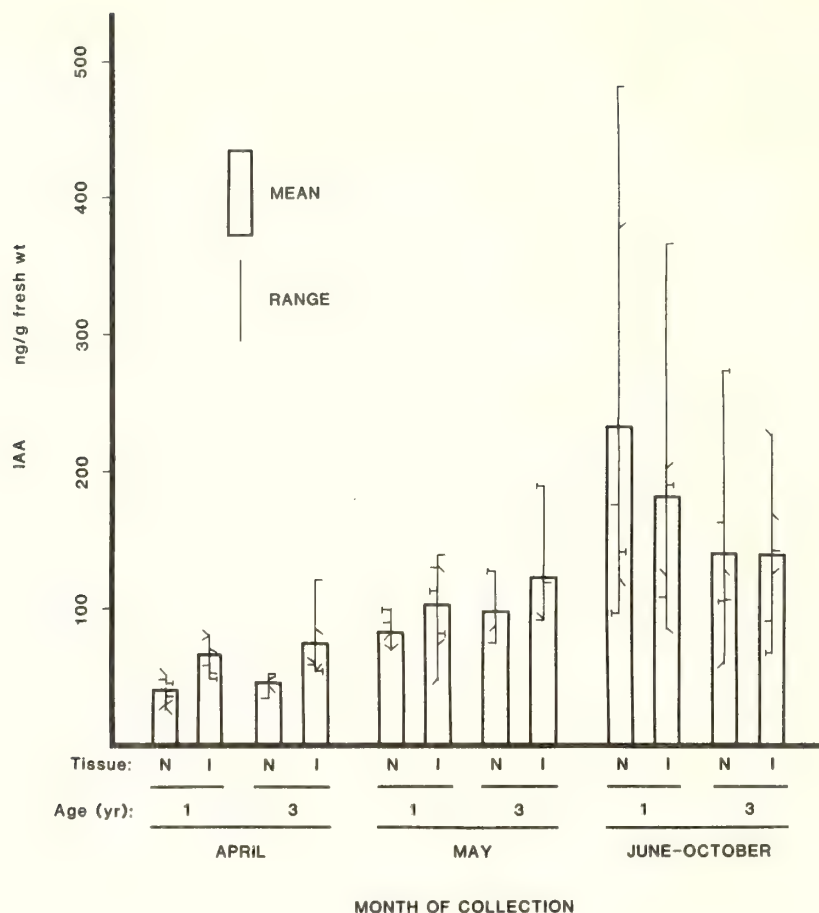
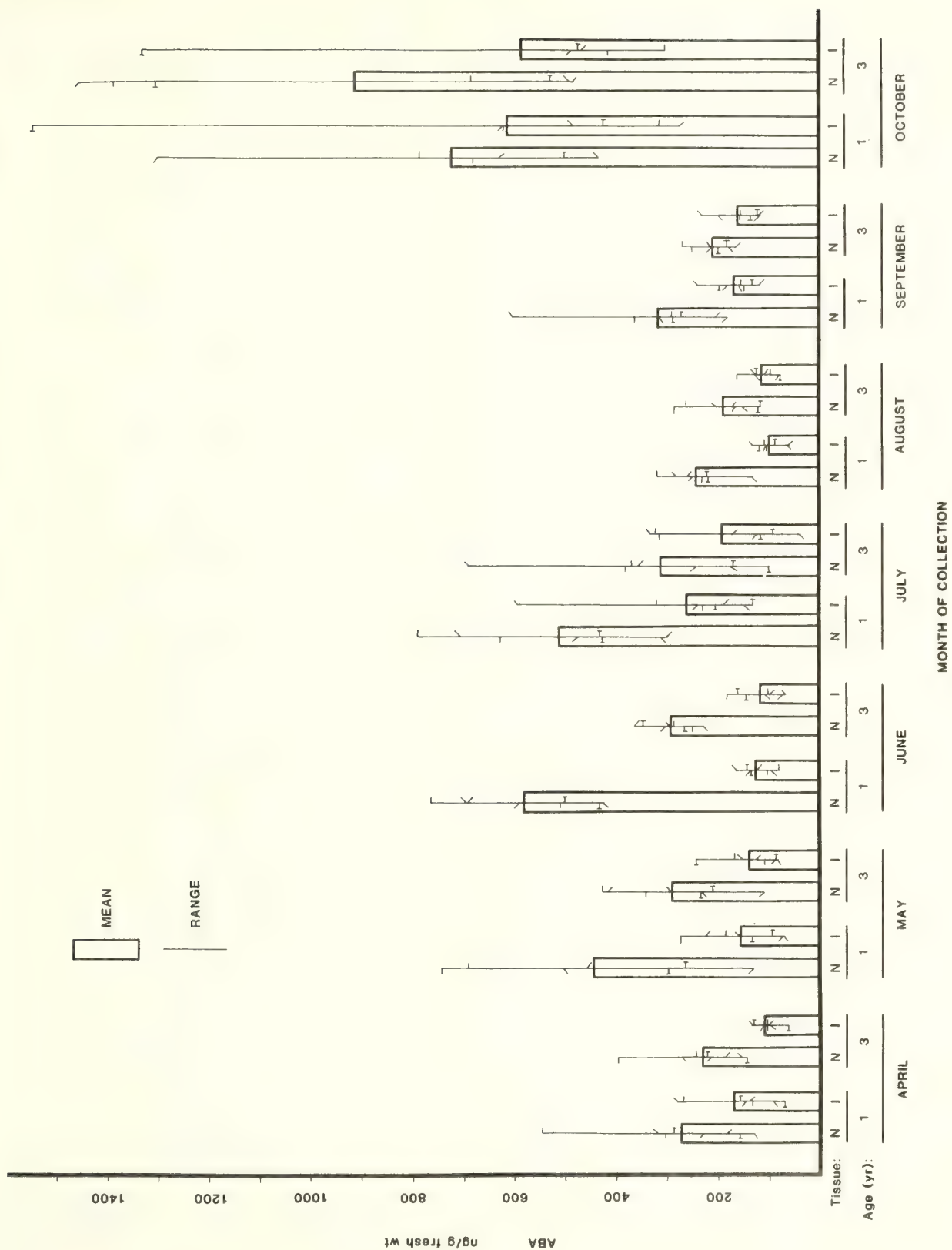


Figure 1.--Amounts (ng/g fresh wt) of indole-3-acetic acid in noninfected branch segments and branches infected with eastern dwarf mistletoe on black spruce. Four different hatch marks (┐ ┌ ∨ ∟), representing data points, on the left side of the range bars represent male infections, right side hatch marks represent female infections. The same type of hatch mark on the same side of the four range bars in a given month represent samples obtained from the same tree. Missing hatch marks indicate missing values. N=noninfected, I=infected, 1=branch segment formed 1 yr previously, 3=branch segment formed 3 yr previously.

Figure 2.--(following page). Amounts (ng/g fresh wt) of abscisic acid in noninfected branch segments and branches infected with eastern dwarf mistletoe on black spruce. Four different hatch marks (┐ ┌ ∨ ∟), representing data points, on the left side of the range bars represent male infections, right side hatch marks represent female infections. The same type of hatch mark on the same side of the four range bars in a given month represent samples obtained from the same tree. Missing hatch marks indicate missing values. N=noninfected, I=infected, 1=branch segment formed 1 yr previously, 3=branch segment formed 3 yr previously.



in the spring and confirms previous observations made on trees during this time of year (Alvim et al. 1976, Hewett and Wareing 1973, Paquet 1979).

Observed increases in zeatin riboside associated with dwarf mistletoe infection is consistent with the hypothesis that increased cytokinin activity is associated with growth changes that occur with dwarf mistletoe infection (Knutson 1979, Paquet 1979, Schaffer et al. 1983) and with growth changes that occur in other plant diseases (Dekhuijzen 1976, Sequeira 1973). Cytokinins have been implicated in controlling the outgrowth of lateral buds (Phillips 1975), and therefore are probably involved in the loss of apical dominance and the resulting witches' broom formation associated with dwarf mistletoe infection. Cytokinins also promote cell division associated with gall formation of other diseases (Dekhuijzen 1976, Sequeira 1973) and could be involved with the stem swellings associated with dwarf mistletoe infection. The mobilization of nutrients to areas of the leaf with higher cytokinin concentrations results in green island formations are commonly observed with leaf parasites (Dekhuijzen 1976, Sequeira 1973). Cytokinins could be involved with the increased partitioning of nutrients to dwarf mistletoe infected tissue. However, it was concluded with another parasitic plant, dodder (*Cuscuta* spp.), that cytokinins were not involved in the partitioning and uptake of nutrients from the host to the parasite (Jacob et al. 1975).

IAA.--IAA concentrations in April and May were consistently higher in black spruce tissue infected with dwarf mistletoe than noninfected tissue. This trend did not continue for the remaining sample periods, but this could be due to the low number of quantifiable samples. More data are needed to ascertain how IAA concentrations vary in dwarf mistletoe infections during the growing season. The concentrations of IAA observed in this study (28-479 ng/g fresh wt) were lower than those measured in other conifer tissue (1000-2000 ng/g dry wt for sitka spruce (*Picea sitchensis*) shoots (Little and Wareing 1981) and 5-720 ng/g fresh wt for Douglas-fir shoots (DeYoe and Zaerr 1976b)). Such differences could be due not only to tree species differences but also to different extraction techniques. Our recoveries of IAA (9.8 to 34.7%) from extracts of conifer tissue were higher than those obtained in other studies (5%, DeYoe and Zaerr 1976; 5-27%, Little et al. 1978).

IAA is closely associated with the control of apical dominance which involves inhibiting the growth of lateral buds and the directed transport of nutrients (Phillips 1975). The increased concentrations of IAA we observed in dwarf mistletoe infections could disrupt the natural balance of IAA in tree stems with the resulting disruption of apical dominance and witches' broom formation. IAA also is associated with cambial activity (Little and Wareing 1981) and with gall formation of other diseases (Pegg 1976a, Sequeira 1973) and could be involved along with cytokinins in the stem swelling associated with dwarf mistletoe infections.

ABA.--The concentrations (37-1546 ng/g fresh wt), monthly variations in concentrations, and recoveries (61-77%) of ABA are similar to those found for shoots of other conifers (Andersson et al. 1978, Webber et al. 1979). When values are compared within trees which were sampled, ABA concentrations were consistently lower in black spruce tissue infected with dwarf mistletoe.

Increases in concentrations of ABA are associated with tissue dormancy, water stress (Milborrow 1974, Walton 1980), and with stunting and wilting of diseased plants (Pegg 1976b). Conversely, reduction in concentrations of ABA are associated with the initiation of bud (Dörfling 1976, Dumbroff et al. 1979) and shoot growth (Webber et al. 1979) in the spring and could have a role in apical dominance (Phillips 1975) and witches' broom formation in dwarf mistletoe infections.

In contrast to the inhibitory effects of ABA, promotive effects of ABA were observed with assimilate sinks (Schussler et al. 1984). Higher concentrations of ABA are associated with assimilate accumulation in seeds and storage tissue. This is consistent with the observations of another parasitic plant, dodder. As in the dwarf mistletoes, dodder is capable of diverting assimilates from other parts of the host to the site of infection (Tsivion 1978, Wolswinkel 1974a). Different portions of the host and *Cuscuta* were assayed for growth inhibitors to wheat seedlings (Ihl and Jacob 1980). The fractions which showed growth inhibition contained ABA. The highest concentration of growth inhibitor was in the haustoria of the dodder, i.e. the site where assimilates are transferred from the host to the parasite. This corresponds with transfer of assimilates into the seed or storage organs where elevated concentrations of ABA are found (Schussler et al. 1984).

ABA concentrations may vary according to the type of nutrient sink. Nutrient sinks associated with active growth of plant tissue and metabolism of assimilates have reduced concentrations of ABA (e.g. buds initiating growth, Dumbroff et al. 1979) while sinks associated with the accumulation of assimilates have high concentrations of ABA (e.g. seeds, Schussler et al. 1984). The situation with dodder may indicate a characteristic that distinguishes the two types of sinks. At the host-parasite interface, nutrients must move across the apoplast from the host phloem cell (Dörfling 1972, Wolswinkel 1974b) from apparently a concentration of low ABA to high ABA (Ihl and Jacob 1980). It is not known if a similar ABA gradient occurs across the apoplastic transfer region in seeds or other storage organs. However, no apoplastic transfer is required for assimilates to enter a region actively growing such as elongating buds and young leaves. Here assimilates enter a region of lower ABA concentration, a condition which may be due to the rapid metabolism of ABA in these actively growing regions (Everat-Bourboulous 1982). We speculate that the symplastic transport of assimilates is directed to lower

concentrations of ABA, but apoplastic transport of assimilates is directed to higher concentrations of ABA. Associating ABA concentrations with variation in transport of assimilates does not imply cause and effect relationships. Whether ABA actually controls assimilate partitioning is not known.

Dwarf mistletoe infections would involve both symplastic and apoplastic transport of assimilates. Dwarf mistletoe infection of conifers stimulates growth resulting in branch swellings and broom formation. Such changes in growth were associated with the lower levels of ABA and increase in the symplastic transfer of assimilates. It would be interesting to investigate the possibility that low levels of ABA in this tissue were due to ABA metabolism. Dwarf mistletoe also has the apoplastic transfer of assimilates between host tissue and endophytic system of the parasite (Alosi 1978, Alosi & Calvin, these proceedings). We hypothesize that the ABA concentrations may be higher in the parasite cells than in the host cells at this interface. Such measurements were not practicle in this study. A test of the hypothesis that ABA is involved in regulating the directed transport of assimilates would be to test if exogenous applications of ABA could disrupt the transport of assimilates from the host to the dwarf mistletoe.

Changes in ABA concentrations in branch segments analyzed in this study are consistent with the hypothesis that symplastic transport of nutrients is directed to lower concentrations of ABA. Noninfected branches (sources of assimilates) show higher concentrations of ABA in one yr old branch segments than three yr old branch segments; the assumed export of assimilate coincides with a decrease in ABA concentrations. In the infected branch where no export of assimilates occurs, no difference in ABA concentration is seen between the two ages of branch segments. The differences in ABA concentrations between the two types of branch segments in the noninfected tissue do not exist in April (before bud break) and October (after dormancy), times of the year when export of assimilates would not be expected.

Additional Considerations.--Mechanisms by which plant growth substances affect dwarf mistletoe infections are complex. In addition to the growth substances already mentioned, gibberellins also are associated with diseases causing abnormal excesses in plant growth (Sequeira 1973) and could be involved in growth changes associated with dwarf mistletoe infections, but such measurements have not been made. Alterations in presence and relative amounts of plant growth substances due to dwarf mistletoe infection will have different impacts on the host. Some effects will be localized (e.g. increase cell division, membrane changes) while others will have more distal effects on the host. Cytokinins have been suggested to regulate one of these distal effects, i.e. directing assimilates from noninfected portions to the infected areas. Data in this paper indicate ABA also could be

involved in assimilate partitioning. Future studies on dwarf mistletoe and plant growth substances should not be restricted to one compound. A good indication on how alterations in plant growth substances will impact tree growth would be to compare the alterations in the various plant growth substances in localized infections of dwarf mistletoe to the alterations of concentrations in systemic infections. The latter infection causes more pronounced changes in host growth.

It is reasonable to expect that several plant growth substances are involved in successful dwarf mistletoe infections, but to understand how these substances influence dwarf mistletoe infections will not be easily attained.

CONCLUSIONS

Dwarf mistletoe infections alter the concentrations of cytokinins, IAA, and ABA in the stem tissue of conifers. There are increases in the concentrations of cytokinins and IAA in conjunction with decreases in ABA concentrations. With what is known about these plant growth substances, such alterations should be associated with sink formation, stem swelling, and loss of apical dominance of the host tissue resulting from dwarf mistletoe infection. Evidence from this study supports the hypothesis that alterations in plant growth substances are involved in successful infections of dwarf mistletoe.

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Water Metabolism and Seedling Photosynthesis in Dwarf Mistletoes¹

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Abstract--Diurnal measurement of host and dwarf Mistletoe transpiration shows that the parasite transpires day and night and at several to many times the host's rate. Chlorophyll content of dwarf mistletoe seeds is low. Still, seedlings consume less O₂ in light than in dark and light fixation of CO₂ probably provides important support for survival.

INTRODUCTION

Mistletoes represent a major stress on their hosts with respect to water loss. In most of the literature to be discussed, the mistletoe out-transpired its host on a surface area or tissue mass basis by a wide margin. Meanwhile, the host usually retained control of its own transpiration by the usual mechanism of stomatal closure during drought or at night.

Perhaps the most vulnerable stage in the life cycle of dwarf mistletoe is the eight to nine month period from expulsion of the fruit from the mother plant to the time when penetration of the new host site occurs. There has been some speculation on the photosynthetic capacity of the seed and resulting seedling based on the visual presence of chlorophyll but only one very brief report of the actual measurement of photosynthetic activity has appeared (Muir 1975). Further studies to quantify chlorophyll content and photosynthetic activity of the fruits and seedlings are obviously needed.

WATER METABOLISM

Literature Review

Recognition came early that mistletoes were a major water drain on their hosts. Kamerling in 1914 used the "detach and weight" method to estimate water loss in *Viscum* and some tropical members of the Loranthaceae (1914a,b). In another report (1914c) he showed that tropical Loranth lost up to 50% more water than their hosts on a surface area basis. The difference in rates

between host and parasite was most dramatic during the hottest part of the day.

A series of studies by Harris and his co-workers from 1916-1934 consisted of measurement of osmotic potential by freezing point depression. They found that expressed sap from the parasite generally had a lower osmotic potential than the sap from the host, except under unusually favorable soil moisture conditions.

Wood (1924) studied *Loranthus* sp. parasitizing *Acacia* in arid regions of Australia. The parasite was lavish in its transpiration, greatly exceeding the host's transpiration.

Korstian (1924) found that osmotic concentrations in three species of *Arceuthobium* and one *Phoradendron* were generally higher than the osmotic concentrations of their hosts.

Vareschi and Pannier (1953) found that two tropical *Phoradendron* spp. did not restrict their transpiration during the dry season, and they reported rates as high as 1.2 g H₂O dm⁻² h⁻¹ for the parasites in both wet and dry seasons.

Struthanthus sp., a tropical loranth, transpired even when its host, *Erythrina* sp., was leafless during the dry season (Marques-Valio et al. 1962). The leaf water content of the parasite was as high in the mornings in the dry season, as it was in the wet season on a surface basis (DeOliveira et al. 1962). The host possessed better control of water loss, and could restrict it more quickly than the parasite. The host had more stomates per surface area than the parasite.

Mark and Reid (1971) measured xylem water potentials of *Pinus contorta* and its parasite *Arceuthobium americanum* in Colorado. Water potential gradients favored the mistletoe obtaining water from the host even when the latter was under considerable water stress. The average water potential of the pine was -14.7 bars, while the average for the mistletoe was -21.3 bars.

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Hellmuth (1971a,b) compared CO_2 fixation and transpiration of the mistletoe *Amyema* sp. parasitic on *Acacia* sp. Net photosynthesis was 50% higher in the parasite than the host, while transpiration during times of water stress was three times the rate of the host. Under moisture sufficient conditions the host slightly out-transpired the mistletoe.

Fisher (1975,1983) carried out extensive experiments on *Arceuthobium-Pinus* water relationships. He used thermocouple psychrometers to monitor the air stream before and after passing through cuvettes enclosing the transpiring tissues. He found that mistletoe transpiration rates were up to four times the rate of the host on a surface area basis. In other experiments, pine seedlings were grown in solution cultures containing varying amounts of polyethylene glycol 4000 as an osmoticum to obtain osmotic potentials ranging from 0 to -15 bars. The *Arceuthobium* spp. generally showed a lower water potential than the host, varying from -3 bars difference with a well watered host to -6 bars difference when the host was in the lowest potential culture solution.

Materials and Methods

Young conifers with mistletoe aerial shoots (*Pinus contorta* and *Arceuthobium americanum*; *P. ponderosa* and *A. campylopodium*; *Tsuga heterophylla* and *A. tsugense*) were grown in peat pots. The surface area of a needle tuft of host pine was measured by counting the needles and measuring the lengths of all needles in the clump and the average diameter of the needle fascicles. The surface area of needles was the outer surface area of the fascicle cylinder plus the flat rectangular areas on the inside of the fascicle. In these pines, stomates occur on all surfaces in approximately equal number per unit area.

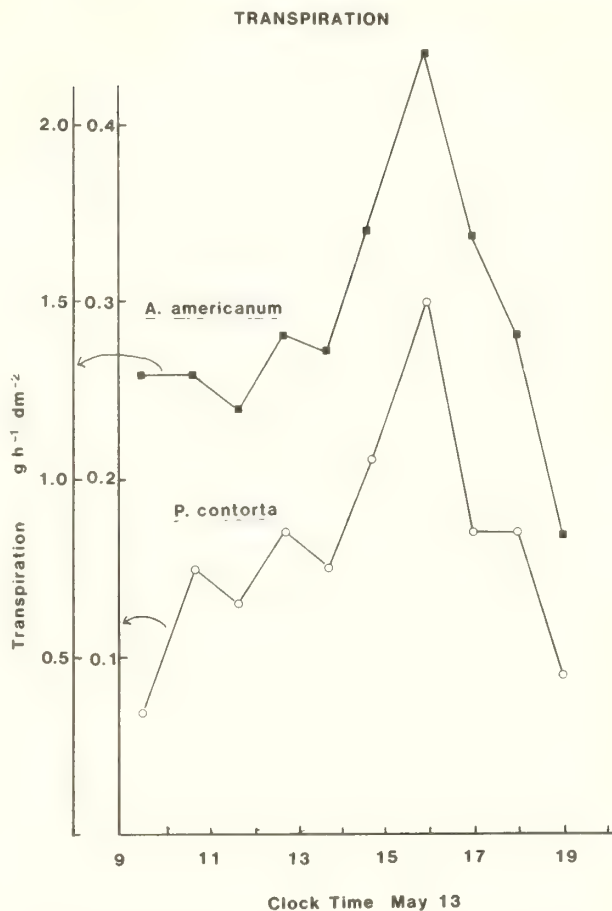
In *Tsuga heterophylla* the number of needles on a branch was counted, lengths were measured and the average needle width determined. The more or less rectangular hemlock needles bear stomates only on the lower surface, so the upper surface was not included in the surface area. A clear sleeve of polyethylene was placed around the parasite aerial shoots or host needles. A piece of rubber tubing was sealed in each open end with plasticene and light string. One tube was open to the air, the tube from the other end of the plastic sleeve led to a dry ice-ethanol trap and a drierite trap and then to a suction pump. Three lines of tubing were used: one from a sleeve enveloping host needles, one from a sleeve around a collection of attached aerial shoots and one pulled ambient air through a pair of traps to provide a correction for the moisture content of the air.

Results

Lodgepole Pine

Figure 1 presents a time course of transpiration of *Arceuthobium americanum* growing on *Pinus*

FIG. 1. COMPARISON OF PINE AND DWARF MISTLETOE



contorta. The rates are expressed as grams of water transpired per square decimeter per hour. The host was well watered. In order to present the data compactly on one graph, two vertical axes are shown, the left one spanning 0-2 g shows rates of the mistletoe transpiration, while the inner vertical axis spanning 0-0.4 g per hour shows the rates of lodgepole pine transpiration. In the early morning the mistletoe transpiration was about 18 times the host rate. Both peak at the same time, 4 PM daylight time, when the mistletoe rate was about seven times that of the host. In this second experiment (fig. 2) the same two vertical axes are used. The host had not been watered for seven days and the pine's transpiration rate at 1:30 PM, just before a thorough watering, was only one-fortieth that of the mistletoe. Over the next two hours the host transpiration recovered to about one-fifteenth the rate of the mistletoe.

Western hemlock

In this experiment the rates of transpiration of western hemlock are compared with *Arceuthobium tsugense* (fig. 3). Since the rates were more comparable than in the pine experiments just shown, the data are referred to only one vertical axis. The host had sufficient water in this experiment. Their rates were approximately equal early in the morning, but by 10 AM the mistletoe

rate exceeded the rate of the host and continued to rise more sharply until early afternoon when the mistletoe transpiration was about 2.3 times the rate of the hemlock. At only one reading (8 AM) did the host transpiration exceed that of the mistletoe.

In another experiment with hemlock (fig. 4) water had been withheld for six days and the hemlock before watering was transpiring only one-tenth to one-half as much as in figure 3 while the mistletoe was actually transpiring 2-3 times more than when water was sufficient. Note that we have two axes here; the inner left hand axis gives hemlock rates, while the mistletoe rates refer to the outer left hand axis. After watering the host's transpiration continued to fall for about an hour before it recovered, and at peak time, about 3 PM daylight time, its rate was only one-half as much as it had been in figure 3. After sunset host transpiration fell to zero and remained there during the night. The mistletoe on the other hand continued to transpire at 2-2.5 $\text{g dm}^{-2} \text{ h}^{-1}$ during the night. The time plotted was the midpoint of the interval, thus the reading shown as 1:15 AM spanned the interval from 11 PM - 03:30 AM. Unfortunately the dwarf mistletoe reading at 10 PM was lost, as excess ice plugged the tube in the dry ice trap stopping the flow of air.

Table I shows variation of transpiration rates with time, and xylem potential measured with a PMS manufactured pressure bomb. The three right hand columns give the transpiration rates of the mistletoe, the host and their ratios, and represent the same data points as the previous time course. Note that at 10 AM, just before watering,

FIG. 2 WATER STRESS AND RECOVERY OF PINE

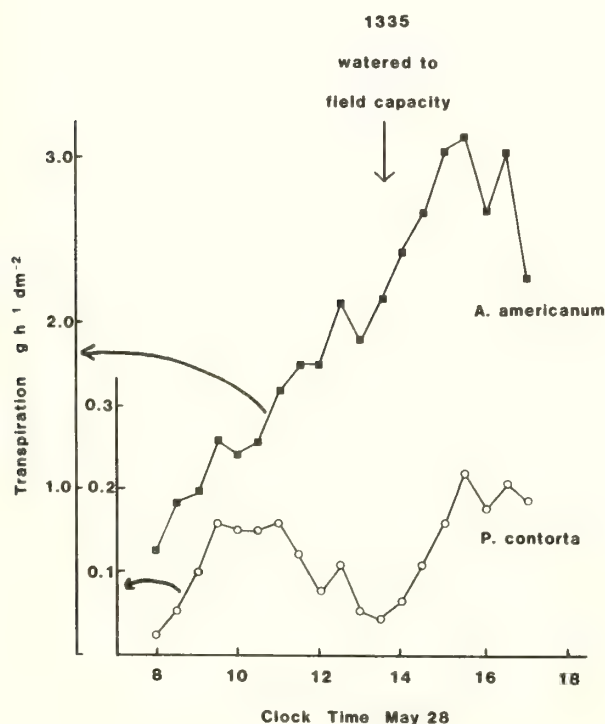
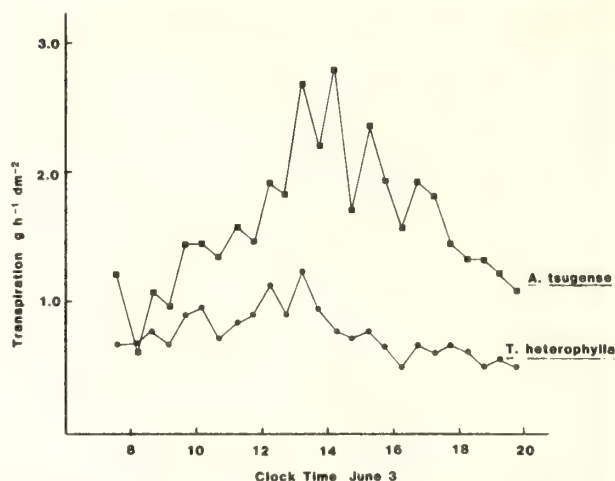


FIG. 3 COMPARISON OF HEMLOCK AND DWARF MISTLETOE TRANSPIRATION



the parasite's transpiration rate was 62 times that of the host!

The xylem pressure potentials were measured several times during the experiment, using freshly detached hemlock twigs or mistletoe aerial shoots from comparable heights on the tree. The paucity of suitable aerial shoots limited the number of samples. During the day the mistletoe had slightly lower pressure potentials but those became strikingly lower at night. The pressure bomb gauge upper limit was 40 bars. The first sample blew out of the chamber as the gauge passed -40 bars. A second sample remained in place, but no moisture had appeared on the cut stem at -40 bars.

Ponderosa pine

The results of a 24 h experiment using a 1.3 m. Ponderosa pine in a 10 gallon peat pot are given in figure 5. The axis values for *Arceuthobium campylopodum* (extreme left axis) are ten times the values for the pine. The pine at this time was probably water stressed. Nighttime transpiration was substantial in both plants--one-third of the peak rate in the day for the pine, and one-half the peak day rate at night for the mistletoe. Just before watering the pot the second morning, a small soil sample was taken from the surface soil in the pot, weighted, oven dried and

Table 1.--Variation of pressure potential and transpiration rate with time.¹

Time	Xylem pressure potential		Transpiration rate		
	Mistletoe	Hemlock	Mistletoe	Hemlock	Ratio
	----- bars -----		--- $\text{g h}^{-1} \text{dm}^{-2}$ -----		
0800	--	--	2.8	0.14	20
1000	--	--	2.6	0.042	62
1020	Watered host to field capacity				
1040	-16	-13.5	3.4	0.34	10
1315	-22.5	-13.5	4.2	0.51	8
1515	-17.5	-12.5	4.6	0.57	8
1730	--	--	4.3	0.51	8
1930	-21.5	-8.5	2.2	0.091	24
0330	-40	-6.5	2.4	0.00	

¹Western hemlock, 0.6 m tall in a 5 gal peat pot; water had been withheld for six days prior to experiment. Transpiration data as in figure 4.

wetted to field capacity. At the time the sample was taken, water content in the soil was 4.9%, or 13% of the soil's field capacity (37% of oven dried weight). This low level of soil moisture did not appear to inconvenience the pine very much as the transpiration rate was increasing before the watering.

SEEDLING PHOTOSYNTHESIS

Literature Review

Most dwarf mistletoes ripen and expel their single seeded fruits from August to October. When they strike a host they cement themselves to it with a hygroscopic pectic material called viscin. Germination occurs in the spring and parasitic contact usually occurs a few weeks later in early summer. Thus, the fruit and subsequent seedling survives up to nine months on its own stored food and photosynthetic capacity. There is some doubt on the period of dormancy required. Wicker (1974) reported that four species of *Arceuthobium* did not germinate immediately after dispersal, but required only about two weeks of cold storage to yield 55-80% germination. In apparent contrast to this, Beckman and Roth (1964) and Knutson (1974) found maximum germination of 50-80% only after 80-180 days of cold storage.

There have been several observations that dwarf mistletoe seeds contain chlorophyll and this has resulted in speculation that the seeds have

photosynthetic capability. Cohen (1963, in a description of the anatomy of the seedling, described the stomates, attributing them with the function of gas exchange during "probably photosynthesis in the green, long-lived seedlings." Kuijt (1969) referred to the chlorophyllous endosperms of the Viscaceae as "seats of great photosynthetic activity." Scharpf (1970) commented on the possibility that photosynthesis occurs in the chlorophyllous seeds, supplying energy necessary for establishment on the host. Muir (1975) did two experiments in which he exposed ten germinated seeds each to ¹⁴CO₂ in light and in dark. He reported that the seeds exposed for 48 hours in light averaged 2,440 cpm and in dark averaged 310 cpm. He concluded that although the amount of CO₂ assimilated was small, it may play a significant role in the supply of energy to the seeds.

Materials and Methods

Chlorophyll was extracted by blending fruits or freeze-dried aerial shoots in 80% acetone for 15 min. with the blender container partly immersed in a cold water bath. Absorbance of an appropriate dilution of the extract was measured in a spectrophotometer and the concentrations determined using the formulæ from Holden (1965).

Respiration and photosynthesis by seedlings were measured by three methods: (1) with a Warburg respirometer with the flasks lighted (8.6 x 10⁴ lux) or darkened with the flasks being

FIG. 4 WATER STRESS AND RECOVERY OF HEMLOCK

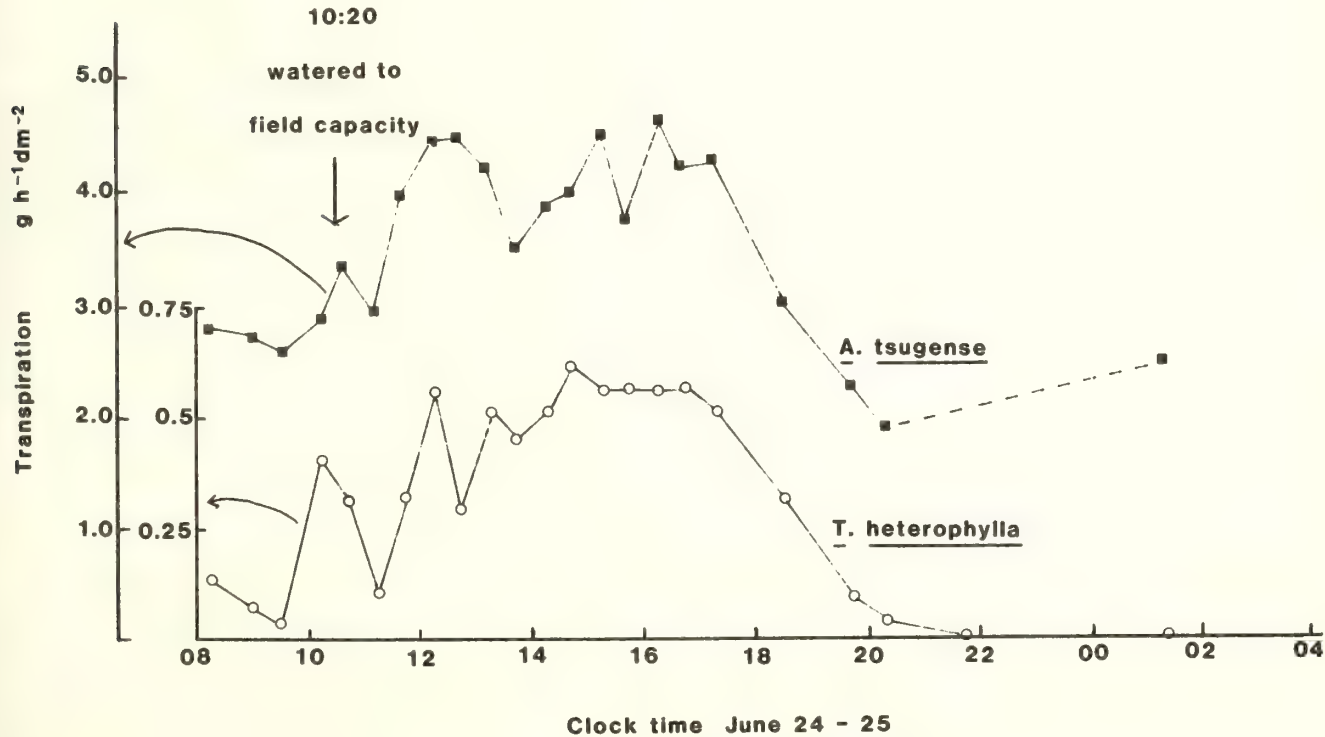
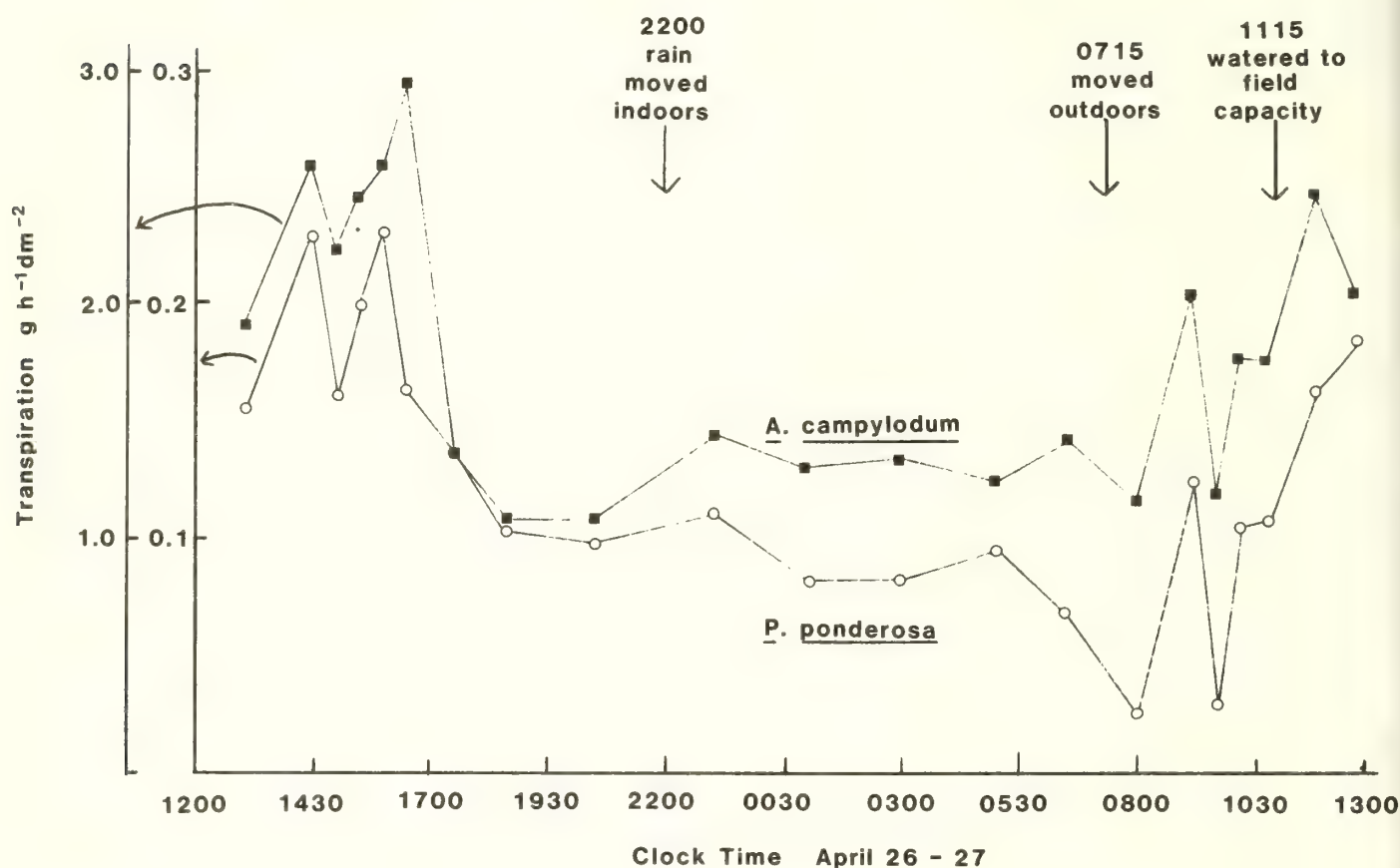


FIG.5 COMPARISON OF PONDEROSA PINE AND DWARF MISTLETOE TRANSPIRATION



wrapped with aluminum foil. The CO₂ level was maintained at 1% with Pardee buffer (Umbreit et al. 1959). (2) polarographically using an oxygen electrode with the seeds immersed in an O₂ saturated solution. Light intensity was 1.3 x 10⁴ lux, or darkness was maintained by wrapping the chamber with heavy cloth. (3) by measuring ¹⁴CO₂ uptake during 24 h in darkness or light (8.6 x 10⁴ lux). The distribution of label was measured by the protocol in figure 6.

Seed germination.--Seeds were collected in the autumns of 1975-77 and stored on filter papers suspended in a closed jar over saturated sodium chloride solution to maintain 75% relative humidity. The jar was kept at 4°C. Two to four months of stratification was given. As needed, seeds were soaked one hour in 2 or 3% H₂O₂, rinsed with sterile distilled water and germinated in petri dishes watered with sterile water. Chlorine bleach diluted to 1-5% reduced germination sharply, but failure to surface sterilize the seeds invariably caused them to be killed by rampant fungus infection. Germination rates were always lower than others have reported--our best rate with the 1976 seed lot was 53%, 1975 seeds gave 30% and 1977 seeds about 12% germination.

Results

The chlorophyll contents of seeds and aerial shoots of the four species analyzed is shown in Table II. Hull and Leonard (1964) reported aerial shoot chlorophyll levels of 0.24-0.48 mg/g tissue for two species of *Arceuthobium*, an amount which represented 12 to 24% of the chlorophyll levels of their hosts. As we will show, the low level of chlorophyll correlates rather well with a low rate of photosynthesis by the seeds.

Table 2.--Chlorophyll content of dwarf mistletoes.

	Seeds ¹		Aerial Shoots ¹	
	chl a+b mg g ⁻¹ FW	a/b ratio	chl a+b mg g ⁻¹ FW	a/b ratio
<i>A. americanum</i>	0.31	1.38	0.35	1.92
<i>A. campylodum</i>	0.34	1.43	0.35	1.50
<i>A. douglasii</i>	0.39	1.35	0.38	2.80
<i>A. tsugense</i>	0.25	1.27	0.31	1.82

¹Each figure is the mean of three or four extracts.

Respiration and Photosynthesis.--These measures were carried out with *A. campylopodum* seedlings which had been started ten days before. Visible germination (radical emergence) occurred three days before. Table III shows the results of three experiments with *A. campylopodum* seedlings, 10 in each Warburg flask. The mean value for O_2 uptake in the dark was $352 \mu l$ per gram, and $204 \mu l$ per gram in the light. We assume that the respiratory quotient (R.Q.) and photosynthetic quotient (P.Q.) are both equal to one, that is that equimolar amounts of O_2 and CO_2 are involved in both dark and light measurements. Subtracting the light rate from the dark rate gives a value of $148 \mu l O_2 g^{-1} h^{-1}$ as the apparent photosynthesis rate, which is equivalent to 42% of the O_2 consumed in dark respiration. Miller and Tocher (1975) reported that aerial shoots of *A. tsugense* showed apparent photosynthesis that was 20-34% of the rate of respiration. Some of this difference might be ascribed to the 10% greater chlorophyll content of *A. campylopodum* seeds as compared with *A. tsugense* aerial shoots.

Polarographic measurements of light and dark O_2 consumption gave closely similar values to the ones we obtained with the Warburg apparatus, $353 \mu l O_2 g^{-1} h^{-1}$ in the dark and $214 \mu l O_2 g^{-1} h^{-1}$ in the light. These figures were the averages of four experiments each.

A respiration rate of $350 \mu l g^{-1} h^{-1}$ is equivalent to $0.688 mg CO_2 g^{-1} h^{-1}$ if the R.Q. is 1.0. If the respiration rate is constant during 24 hours, each seedling loses $48 \mu g CO_2$ or 1.6% of its fresh weight per day. In a 12 h light period each seedling can fix $10 \mu g CO_2$ per day or 21% of the amount lost in 24 h. Photosynthetic carbon fixation may provide the difference between life and death during the few weeks after germination before a food supply from the host can be obtained.

$^{14}CO_2$ Incorporation by *A. Campylopodum* Seedling.--The results from $^{14}CO_2$ labelling of seeds in light and dark and subsequent analysis of location of ^{14}C are reported in Table IV and V. The results show that seeds of *A. campylopodum* assimilated CO_2 in light. CO_2 assimilation in the light was approximately 350 times CO_2 assimilation in the dark. The seeds in light incorporated 25% of the original $^{14}CO_2$ present in the reaction flask during 24 hours. However, it should be remembered that the seeds are respiring at a greater rate than they are photosynthesizing, thus in the course of twenty-four hours substantial

Table 3.--Oxygen uptake by *A. campylopodum* seedlings in light and dark.

Experiment Date	Manometric oxygen uptake ¹	
	Dark (± 1 SD)	Light (± 1 SD)
Feb. 3, 1977	369 ± 42	240 ± 6
Jan. 19, 1978	357 ± 40	108 ± 13
Mar. 23, 1978	330 ± 17	266 ± 46
Mean	352 ± 20	204 ± 85

¹ Data from three to six flasks, each containing 10 seedlings.
microliters of $O_2 g^{-1} h^{-1}$.

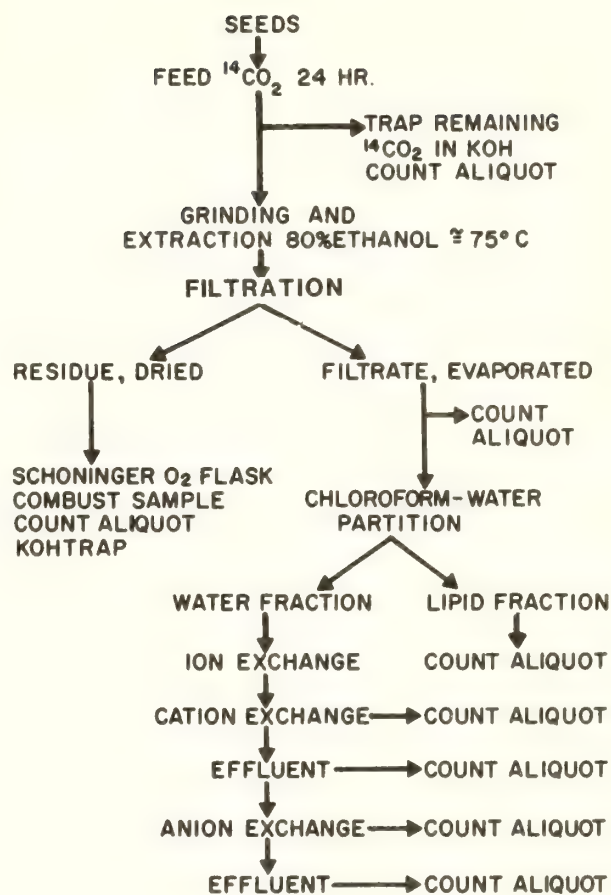


Figure 6. Flow chart for ^{14}C Label Procedure and analysis

Table 4.-- ^{14}C label distribution in *A. campylopodum* seedlings.

Fraction	Dark fixation ¹	Light fixation ²
	dpm	dpm in thousands
Total ^{14}C incorporated	560	342
Solid residue	560	6.5
Ethanol soluble	0	336
Chloroform soluble	0	28
Water soluble	0	214
Not accounted for	0	94

¹Mean of two runs

²Mean of four runs

Table 5.-- ^{14}C Distribution by ion exchange chromatography.

Sample	Cationic	Anionic	Neutral
----- % of water soluble -----			
1	11	29	60
2	25	22	53
3	24	21	55
4	17	15	67
Mean	19	22	59

dilution of the labelled $^{14}\text{CO}_2$ took place. Therefore, quantification of photosynthetic rates of the seeds by this method is not reliable.

Extraction of seeds with ethanol showed that 97% of the incorporated ^{14}C was ethanol soluble, of this, 83-90% of the activity in the ethanol extracts concentrate was H_2O soluble. The H_2O soluble phase was separated into cationic, anionic and neutral fractions by ion exchange chromatography. These results are reported in Table V. The majority (50-67%) of the label remained in the neutral fraction, while 11-25% of the label was in the cationic fraction, and 15 to 29% of the label was in the anionic fraction.

Miller and Tocher (1975) reported the following values from ion exchange chromatography of water soluble ^{14}C from aerial shoots: cationic fraction, 12-26%; anionic fraction, 20-25%; and neutral fraction, 51-68%. Hull and Leonard (1964) reported a smaller percentage (one percent) of label in the cationic fraction, and a larger percentage (36-70%) in the anionic fraction. They suggested the presence of Crassulacean acid metabolism (CAM) or of enzymes active in CAM in aerial shoots based on the large amounts of ^{14}C label incorporated into malic acid. The non-existent to very minute assimilation of ^{14}C by the seeds of *A. campylopodum* in the dark suggests the absence of CAM.

Tainter (1971) suggests that chloroplasts of *A. pusillum* resembled chloroplasts associated with C_4 carbon assimilation systems. The C_4 pathway is usually associated with a certain type of cell anatomy within leaves. Mesophyll cells have chloroplasts which fix CO_2 by PEP carboxylase to form malate. The malate is either directly transferred or is aminated to form aspartate and then transferred to the bundle sheath cells. In the bundle sheath cells the CO_2 carrier is decarboxylated. The CO_2 is then fixed in the chloroplast via the Calvin cycle (Bonner and Varner 1976). This elaborate anatomy has not been reported to occur in dwarf mistletoes. However, that does not exclude the possibility of the presence of C_4 system enzymes. It is apparent that further investigation of the pathway of carbon fixation in the seed is needed.

CONCLUSIONS

Water Metabolism.--Thus, we can say that the tree dwarf mistletoes studied, *A. americanum*, *A. campylopodum* and *A. tsugense* out-transpire their hosts under almost all conditions of soil moisture stress or darkness. Moreover the transpiration rates observed were usually several to many times the rates of the hosts, particularly when host stress was greatest. The only exception was *A. tsugense* when its host was well supplied with water.

Seedling Photosynthesis.--Seeds of *a. campylopodum* were quite vulnerable to fungal attack during incubation in the laboratory. Presoaking of seeds with two and three percent

H_2O_2 resulted in less fungal contamination and in relatively high germination percentages as compared to results obtained using Chlorox pretreatments. The seeds were found to contain chlorophyll in concentrations (0.25 to 0.40 mg/g fresh weight) comparable to those in aerial shoots which are ten to twenty percent the amounts found in host leaves (Hull and Leonard 1964). The variance in chlorophyll concentrations in seeds and aerial shoots of different species supports the hypothesis of Miller and Tocher (1975) that different species of *Arceuthobium* vary in their dependence upon the host.

O_2 consumption by seeds in light and in dark was measured by manometric and polarographic methods. The resulting data showed good agreement. The difference between the light and dark rates was attributed to O_2 evolved during photosynthesis. This mean difference equaled $148 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$. This figure equaled 42% of the dark respiration rate of $352 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$. The ^{14}C labelling experiments proved that the seeds fix CO_2 in the light. This CO_2 fixation in light supports the previous reasoning that the difference between O_2 uptake in the light and in the dark was attributed to O_2 evolved in the light reactions of photosynthesis. Further investigation of the pathway of CO_2 fixation in seeds and shoots of dwarf mistletoe is warranted.

This study supports the earlier hypothesis of Cohen (1964), Kuijt (1969), and Scharpf (1970), that the chlorophyll present in dwarf mistletoe seeds is functional. However, Kuijt (1969) appears to have been overly enthusiastic in his description of Viscacean seeds as "seats of great photosynthetic activity."

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Host Resistance to Dwarf Mistletoes¹

Robert F. Scharpf²

Abstract.--Resistance to dwarf mistletoes (*Arceuthobium*) is expressed mainly by varying degrees of infection among host species. Some resistance occurs within certain dwarf mistletoe-host species combinations, however. Such resistance appears to result from both morphological and physiological characteristics of the hosts.

Resistance of certain coniferous tree species to infection by dwarf mistletoes (*Arceuthobium*) has been recognized for nearly as long as investigators have been observing and studying these parasites in the field. Many dwarf mistletoes have definite host preferences. And yet infection occasionally is found on tree species other than the primary host. One of the first taxonomic systems of classification was based on host relationships without regard for "biological parity" (Gill 1935). A later taxonomic classification of the taxa is based on morphological characteristics (Hawsworth and Wiens 1972). In spite of the morphological integrity of most dwarf mistletoes, Hawsworth and Wiens (1972) recognize definite host preferences by the various species and subspecies and use them to help identify the taxa. They devised a "susceptibility class" system based on the percentage of trees of a species that are infected within 20 feet of an infected "main" or "principal" host (table 1). This classification system rates the relative susceptibility (resistance) of hosts to dwarf mistletoe species in the forest.

In nature, about two-thirds of the dwarf mistletoes parasitize species other than their principal hosts. Infection of these other hosts is highly variable and often difficult to explain. A species like *A. laricis* in the western United States, for example, occurs on members of at least four other genera in the Pinaceae, whereas *A. apachecum* and *A. blumeri* are found only on *Pinus strobiformis* (southwestern white pine). Strange host relationships that defy the imagination also have been observed (table 2). For instance, in mixed conifer stands in California, *A. abietinum* f. sp. *concoloris* growing on *Abies concolor* (white fir) cannot infect *A. magnifica* (red fir), and *A.*

abietinum f. sp. *magnificae* growing on red fir cannot infect white fir in stands where abundant opportunity exists for them to do so (Parmeter and Scharpf 1963). But, *A. abietinum* f. sp. *concoloris* can occasionally infect *Pinus lambertiana* (sugar pine), *P. contorta* (lodgepole pine), and *P. monticola* (western white pine). In addition, when these unusual hosts are infected, more than one infection often occurs. These strange crosses often result in an "all or nothing" mode of parasitism of the tree (Hawsworth and Wiens 1972). For example, *Picea engelmannii* (Engelmann spruce) is rarely parasitized by *A. americanum*, but when it is, it often bears 100 or more infections per tree (Hawsworth and Graham 1963). Why certain dwarf mistletoes cannot infect a closely related host species but can cause severe infection of trees of a different genus remains a mystery.

To further confound our understanding of resistance, large geographic areas of apparently susceptible, native host species are uninfected by dwarf mistletoes, whereas other areas are heavily infected. Absence of *A. vaginatum* on *P. ponderosa* (ponderosa pine) in the Black Hills area of South Dakota (Hawsworth 1963), and lack of *A. douglasii* on *Psuedotsuga menziesii* (Douglas-fir) along much of the Pacific coast (Wicker 1969) are examples of this phenomenon. Why these hosts are free of dwarf mistletoe in these locations and infected in others is not fully known, but certain climatic factors appear to play an important role in some cases.

The lack of resistance to dwarf mistletoe among some introduced, conifer species planted within the range of dwarf mistletoes in the field (table 3) is an equally perplexing problem. A striking example of this was a 55-year-old plantation of *P. sylvestris* (Scotch pine) that became heavily infected by larch dwarf mistletoe, *A. laricis* in Washington (Graham and Lephart 1961). In contrast, several native tree species that are immune or highly resistant to infection by dwarf mistletoes in the field have been infected by inoculation under artificial conditions (table 4). Why certain species are resistant in the field but susceptible under artificial conditions is not known. Perhaps certain climatic conditions or biotic factors in nature preclude infection.

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Table 1.--Five classes used to rate the relative susceptibility of hosts to dwarf mistletoes.

Host Class	Infection Factor	Remarks
I. Principal	At least 90 percent; usually nearly 100 percent	Uninfected trees are seldom found within the 20-foot zone unless they are small and stunted
II. Secondary	50 to 90 percent	--
III. Occasional (or tertiary)	5 to 50 percent	--
IV. Rare	More than 0 but less than 5 percent	--
V. Immune	0	Potential host trees not infected even where the dwarf mistletoe in question is common

Source: Hawksworth and Wiens (1972)

Table 2.--Reported incompatible host-parasite relationship.¹

Arceuthobium	Host	Reference
<u>A. abietinum</u> f. sp. <u>concoloris</u>	<u>Pinus contorta</u> subsp. <u>murrayana</u>	Hawksworth & Wiens 1982
<u>A. abietinum</u> f. sp. <u>concoloris</u>	<u>Pinus lambertiana</u>	Hawksworth & Wiens 1972
<u>A. americanum</u>	<u>Picea pungens</u>	Hawksworth & Wiens 1972
<u>A. americanum</u>	<u>Pinus albicaulis</u>	Wier 1919b
<u>A. americanum</u>	<u>Pseudotsuga menziesii</u>	Hawksworth & Wiens 1972
<u>A. pusillum</u>	<u>Larix laricina</u>	Tainter & French 1967
<u>A. tsugense</u>	<u>Larix europaea</u>	Kuijt 1964
<u>A. tsugense</u>	<u>Larix occidentalis</u> ²	Smith 1974
<u>A. tsugense</u>	<u>Picea engelmannii</u>	Hawksworth & Wiens 1972
<u>A. tsugense</u>	<u>Picea sitchensis</u>	Laurent 1966

¹ Updated from Hawksworth and Wiens (1972)

² Inoculations

In a few instances, infection of a host by one species of dwarf mistletoe seems to "exclude" or prevent infection by others (Hawksworth 1968; Hawksworth and Wiens 1972). For example, when P. contorta ssp. latifolia (lodgepole pine) is the principal host for A. americanum, A. cyanocarpum has

not been found; and in stands where lodgepole pine is the principal host for A. cyanocarpum, A. americanum does not occur (Hawksworth 1968). Another type of exclusion of infection by dwarf mistletoes has also been observed in some instances, but in this case members of the same species are

Table 3.--Reports of extra-limital hosts naturally infected by dwarf mistletoes.¹

Host	<i>Arceuthobium</i>	Locality	Reference
<i>Cupressus macrocarpa</i>	<i>A. oxycedri</i>	USSR	Zefirov 1955
<i>Juniperus thuifera</i>	<i>A. oxycedri</i>	USSR	Lazarev & Grigonov 1980
<i>Larix europaea</i>	<i>A. tsugense</i>	British Columbia	Kuijt 1964
<i>Picea abies</i>	<i>A. laricis</i>	Idaho	USDA 1963
<i>P. pungens</i>	<i>A. pusillum</i>	Maine	USDA 1960
<i>Pinus banksiana</i>	<i>A. laricis</i>	Idaho	Graham 1959a
<i>P. pinaster</i>	<i>A. campylopodum</i>	California	Kuijt 1960b
<i>P. halapensis</i>	<i>A. campylopodum</i>	California	Scharpf ²
<i>P. resinosa</i>	<i>A. laricis</i>	Idaho	USDA 1962
<i>P. sylvestris</i>	<i>A. laricis</i>	Washington	Graham & Leaphart 1961
<i>P. sylvestris</i>	<i>A. americanum</i>	Washington	Graham & Leaphart 1961
<i>P. sylvestris</i>	<i>A. americanum</i>	Alberta	Powell 1968
<i>P. sylvestris</i>	<i>A. campylopodum</i>	Idaho	Weir ³
<i>P. sylvestris</i>	<i>A. vaginatum</i>	Colorado	Hawksworth & Laut 1981

¹Updated from Hawksworth and Wiens (1972)

²Unpublished data by Robert F. Scharpf

³Unpublished data by J. R. Weir

also excluded. Infected branches are usually highly resistant or immune from secondary infection by either the same or other dwarf mistletoe species (Hawksworth and Wiens 1972). The mechanisms by which dwarf mistletoes exclude one another are not known and is a fascinating area for further research.

In unusual host-parasite combinations, resistance is often expressed by certain growth responses of the mistletoe and morphological changes in the host. For instance, with infection of sugar pine by white fir dwarf mistletoe, shoots of the parasite develop slowly and are sparse, endophytic system growth appears slow, and excessive branch swelling occurs. Similar expressions of host-parasite incompatibility have been reported for other odd dwarf mistletoe-host combinations as well (Hawksworth and Wiens 1972).

PROBLEMS IN DETERMINING RESISTANCE

With a parasitic plant as widespread and as intensively observed and studied as the dwarf mistletoes, one would expect several clearcut examples of resistance of host species to a given dwarf mistletoe. But determining resistance from field observation alone can be a very questionable if not erroneous practice. As an example of the problem, one of the earliest tests of reportedly resistant ponderosa pines to *A. vaginatum* ssp. *cryptopodum* failed to show any differences between resistant and susceptible trees (Hawksworth and Edminster 1981). In these tests, several hundred progeny from "resistant" and "susceptible" trees were outplanted in 1932 for testing in a naturally

infested stand. A check of the surviving trees in 1959 showed that some were lightly to moderately infected and possibly resistant. However, another examination in 1979, showed the "resistant" trees did not differ significantly from "susceptible" trees in survival rate, percentage of trees infected, and average rated level of infection. In this case, it took nearly a half century of field testing to show that the initial field determinations of what constituted "resistant" trees were in error.

What are some of the problems in determining resistance of a host to a given dwarf mistletoe? The assumption that populations or geographic areas of trees that are free of infection are resistant to dwarf mistletoes is almost certain to lead to error. As previously discussed, large (and small) stands of susceptible hosts are often disease-free for unknown reasons. Climatic limitation of the parasite from portions of the host range has been suggested as a reason for this difference (Hawksworth 1956, 1963; Wicker 1969).

Geologic history is another factor that has regulated spread of dwarf mistletoe. For example, the absence of dwarf mistletoe in most of the stands around Sunset Crater, a volcano in Arizona that erupted about 900 years ago (Hawksworth 1960), illustrates how geologic history can confuse determinations of resistance based on field observations. In this case, the host was able to become reestablished on the site after the eruption more rapidly than the parasite was able to reinvade the new stands.

Because of the mechanism of spread of dwarf mistletoe, individual trees or groups of trees often escape infection, giving the appearance of

Table 4.--Extension of host ranges of Arceuthobium as determined by artificial inoculations on unnatural hosts.

Host	Dwarf mistletoe	Reference
<u>Abies amabilis</u>	<u>A. laricis</u>	Smith & Wass 1972b
<u>A. concolor</u>	<u>A. campylopodum</u>	Weir 1918a
<u>A. grandis</u>	<u>A. campylopodum</u>	Weir 1918a
<u>Larix europaea</u>	<u>A. laricis</u>	Weir 1918a
<u>L. leptolepis</u>	<u>A. laricis</u>	Weir 1918a
<u>L. occidentalis</u>	<u>A. campylopodum</u>	Weir 1918a
<u>L. occidentalis</u>	<u>A. tsugense</u>	Smith 1970a
<u>Picea abies</u>	<u>A. campylopodum</u>	Weir 1918a
<u>P. abies</u>	<u>A. tsugense</u>	Smith 1965
<u>P. glauca</u>	<u>A. laricis</u>	Smith 1974
<u>P. glauca</u>	<u>A. tsugense</u>	Smith 1965
<u>P. engelmannii</u>	<u>A. tsugense</u>	Smith 1970b
<u>P. pungens</u>	<u>A. tsugense</u>	Hawksworth & Wiens 1972
<u>Pinus banksiana</u>	<u>A. occidentale</u>	Hedgcock & Hunt 1917
<u>P. bungeana</u>	<u>A. occidentale</u>	Hedgcock & Hunt 1917
<u>P. flexilis</u>	<u>A. apachecum</u>	Mathiasen 1978
<u>P. flexilis</u>	<u>A. blumeri</u>	Mathiasen 1978
<u>P. flexilis</u>	<u>A. microcarpum</u>	Mathiasen 1978
<u>P. mugo</u>	<u>A. campylopodum</u>	Weir 1918a
<u>P. palustris</u>	<u>A. occidentale</u>	Hedgcock & Hunt 1917
<u>P. pinea</u>	<u>A. occidentale</u>	Hedgcock & Hunt 1917
<u>P. ponderosa</u>	<u>A. tsugense</u>	Smith & Craig 1968
<u>P. radiata</u>	<u>A. tsugense</u>	Smith & Craig 1968
<u>P. resinosa</u>	<u>A. campylopodum</u>	Weir 1918a
<u>P. strobiformis</u>	<u>A. cyanocarpum</u>	Hawksworth & Wiens 1972
<u>P. strobis</u>	<u>A. cyanocarpum</u>	Hawksworth & Wiens 1972
<u>P. sylvestris</u>	<u>A. campylopodum</u>	Weir 1918a
<u>P. sylvestris</u>	<u>A. tsugense</u>	Smith & Craig 1968
<u>P. torreyana</u>	<u>A. occidentale</u>	Kuijt 1960a
<u>P. virginiana</u>	<u>A. occidentale</u>	Hedgcock & Hunt 1917
<u>Pseudotsuga menziesii</u>	<u>A. tsugense</u>	Smith & Wass 1972a
<u>Tsuga canadensis</u>	<u>A. tsugense</u>	Weir 1918a

¹Updated from Hawksworth and Wiens (1972)

resistance. Adequate levels of inoculum (dwarf mistletoe seeds) and the presence of a suitable target are necessary for infection to occur (Wicker 1967, Wicker and Shaw 1967). In many cases, hosts are screened from seeds by non-host trees, wind patterns distribute seeds in unusual ways, and many variables can affect the inoculum before infection takes place.

In spite of these problems, several investigators have reported what they consider to be examples of resistance to dwarf mistletoes in the field. For example, in a study of infection of ponderosa pines by A. campylopodum in California, about 1 in 23 trees appeared to show some resistance to infection (Wagener 1965). In another study, one seed source of P. jeffreyi (Jeffrey pine) in an infected plantation showed noticeable resistance to infection (Scharpf and Parmeter 1967). Similarly, two instances were noted in which individual ponderosa pines in the southwest appeared resistant

to A. vaginatum ssp. cryptopodum (Hawksworth 1961). But the mechanism by which the trees in these cases resisted infection was not known, however. An interesting mechanism of resistance to A. campylopodum has been observed in ponderosa pine (Roth 1966). A "drooping" needle race of ponderosa pine is quite resistant because the seeds of dwarf mistletoe slide off the host rather than adhere and cause infection. In this case, a morphological characteristic of the host rather than a physiological response to infection imparts some level of resistance.

SELECTION AND TESTING FOR RESISTANCE

Relatively little effort has gone into selecting and testing for resistance to dwarf

Table 5.--Number of *A. campylopodum* plants developing on grafted ponderosa pines and on seedlings interplanted as controls. Progenitors of the grafts ("candidates") were selected for mistletoe resistance.

Test Clones	Number of trees	Mean Tree Height	Total Plants on all trees	Range among individual trees	Average plants per tree
		-cm-		number	
Resistant clone 1	13	62	0	0-0	0.0
Resistant clone 2	8	66	11	0-4	1.4
Resistant clone 3	5	66	1	0-1	0.2
Resistant clone 4	4	70	0	0-0	0.0
Resistant clone 5	5	88	18	0-10	3.6
Resistant clone 6	4	80	20	4-8	5.0
Resistant clone 7	3	51	1	0-1	0.3
Susceptible grafts	9	63	55	0-16	6.1
Deschutes nursery stock	27	84	433	6-43	16.0
Colorado nursery ¹ stock	10	77	134	2-32	13.4

Source: Roth (1974a)
¹*P. ponderosa* var. *scopulorum*

mistletoes. Locating potentially resistant trees is a difficult task, and many managers believe that they can control damage from dwarf mistletoe with silvicultural methods (Roth 1974a).

A few deliberate efforts to find resistance to dwarf mistletoes have been undertaken. Hawksworth and Edminster (1981), failed to find any indication of resistance by ponderosa pine to *A. vaginatum* ssp. *cryptopodum* in a test begun in 1932. Some differences in resistance of ponderosa pine and Jeffrey pine to *A. campylopodum* have been shown in two more recent studies. In one, small potted ponderosa pines were grafted with "resistant" scions, placed in an infected stand, inoculated with seeds for 5 years, and examined for several years thereafter for infection (Roth 1974a). Results showed not only clear differences in resistance to infection among the test trees, but also differences in susceptibility to damage (table 5, figure 1). The mechanism of resistance in these tests was not determined, but only current years' tissues of ungrafted seedlings were regularly infected in contrast to less regular infection of shoots of more mature scions. Roth (1974a) suggested that anatomical features accompanying shoot differentiation are involved in resistance, but that physiological resistance cannot be overlooked. In a related study, ponderosa pine showed juvenile susceptibility to dwarf mistletoe (Roth 1974b). Scions from trees of various ages grafted to seedlings showed a decrease in frequency of infection with an increase in tree age. Susceptibility of trees of various ages has not been tested in the field, however. In contrast to Roth's findings on pine, I found small true firs in the field in California to be more resistant to infection than larger ones. In this study, tree size rather than age was more closely associated with infection. The mechanism by which small trees

resisted (or escaped) infection was not determined (Scharpf 1969).

The most recent tests to determine resistance of a host species to dwarf mistletoe are in progress in California. They are being conducted with a "resistant" seed source of Jeffrey pines (Scharpf and Parmeter 1967). In these tests, several approaches to determine resistance are being used. In the first approach, two plantations of Jeffrey pines planted nearly a half century ago adjacent to naturally infested overstory trees are being monitored about every 5 years for differences in susceptibility among various Jeffrey pine seed sources, starting in 1961. Resistance has continued

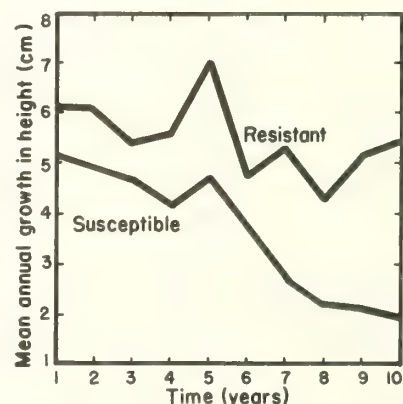


Figure 1.--Mean annual growth in height of clonal members from candidates 1, 3, 4 and 7, compared with susceptible controls and with nursery stock of "Deschutes" and "Colorado" seed sources (Roth 1974a).

to be found in one specific seed source. Periodic monitoring of these plantations will help determine if resistance persists over time.

The second approach to testing for resistance was begun in 1980 in another plantation of Jeffrey pines established with the same seed sources in the other study. These pines (7 years old in 1980) were ideal size for carefully controlled inoculation tests. In 1980 and 1981, about 15000 dwarf mistletoe seeds were placed on tree branches and followed for infection. Although results are preliminary at this time, the "resistant" seed source shows a level of resistance several times that of the more susceptible sources (table 6). Because at least one seed source of Jeffrey pine is consistently showing high levels of resistance, further research is underway to determine the mechanism(s) of resistance.

The third approach involves growing seedlings of the "resistant" Jeffrey pine and outplanting them along with the local seed source as controls, in naturally infested stands. One outplanting was established in Southern California in spring 1984, and more are planned for other areas in the future. With more research on mechanisms of infection, with the examination of existing field tests for several more years, and with outplanting of resistant and native seed sources in various areas, levels of resistance of several seed sources of Jeffrey pines should be established.

CONCLUSIONS

Control of dwarf mistletoes is now most often accomplished by silvicultural methods of forest management. Treatments usually include removal of the infected species in a mixed species forest through thinning or harvest, or by clearcutting

Table 6.--Infections occurring on different seed sources of Jeffrey pine inoculated with *A. campylopodum* at Institute of Forest Genetics, Placerville, California, 1980-1981.

Jeffrey pine seed source (California)	Number of infections (9/83)	Percent of all infections
High elevation, east side Sierra Nevada (Alpine Co. 8000 ft)	106	57
Lake Tahoe (Eldorado Co. 5500 ft)	61	33
West side Sierra Nevada (Placer Co. 3500 ft)	18	10
Total	185	100

areas where heavy infection occurs in pure species stands. Unfortunately, not all stands can be clearcut or managed in ways to eliminate dwarf mistletoes or to avoid damage from these parasites. The availability of resistant planting stock would be an important addition to control options, particularly in cases where high values are at stake or where alternate tree species are not suitable or available.

Further studies are needed to identify resistant candidate trees or dwarf mistletoe resistant seed sources in the field. New methods or techniques need to be developed to "speed up" the process for screening and testing resistant selections. Further investigation is needed to better understand the mechanisms that impart resistance to trees. And, basic research is needed to provide information about the inherent characteristics of dwarf mistletoes and their hosts that will aid in selection and development of resistance.

With the continuing emphasis on intensive forest management and with increasing constraints on land use and management options, the development of dwarf mistletoe resistant conifers should be pursued as another approach to control these serious pathogens in Western North America.

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Seed Development, Germination Behavior and Infection Characteristics of Several Species of *Arceuthobium*¹

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Abstract.--Seeds of *Arceuthobium* species account for 5-18% of mature fruit weight. Viscin accounts for 26-61% of mature seed weight. Repeated wet-dry cycles of mistletoe seeds reduce the water-holding capacity of viscin. Seed germination is improved with light and with time since harvest. Radicle elongation was 24-92 micrometers per day. *Arceuthobium* seeds are negatively phototropic, positively thigmotropic, and geotropically neutral. Greatest infection was at a low temperature-high light regime, but growth of both infected and uninfected trees was best at a high temperature regime. Growth of aerial shoots of *A. campylopodum* was best at the high temperature regime.

INTRODUCTION

Information reported here deals with observations on the basic biology of species of *Arceuthobium* native to Oregon. An original intent was to develop a body of information on the behavior of these species so they could be manipulated with some predictability. The plan was to develop greenhouse "model forests" of infected and uninfected seedlings which would be correlated with real-world stands and to develop management recommendations based on their responses to stresses and manipulations.

Before being forced to abandon this work, we developed a considerable body of data on the biology of *Arceuthobium* seeds. Since much of the work was not completed, we cannot draw statistical inferences from the data. However, the data obtained are biologically sound and were carefully collected. It is reported here in the hope that it will help develop a more complete understanding of the fascinating genus *Arceuthobium*.

The six Oregon dwarf mistletoes studied and their principal hosts are (1) *Arceuthobium*

abietinum Engelm. ex Munz f. sp. *concoloris* (hereafter abbreviated as *A. abietinum*) (on *Abies grandis* (Dougl. ex D. Don) Lindl.), (2) *A. americanum* Nutt. ex Engelm. (on *Pinus contorta* Dougl. ex Loud.), (3) *A. campylopodum* Engelm. (on *Pinus ponderosa* Dougl. ex Laws.), (4) *A. douglasii* Engelm. (on *Pseudotsuga menziesii* (Mirb.) Franco), (5) *A. laricis* (Piper) St. John (on *Larix occidentalis* Nutt.), and (6) *A. tsugense* (Rosendahl) G. N. Jones (on *Tsuga heterophylla* (Raf.) Sarg.). The research was conducted at the U.S. Forest Service Forestry Sciences Laboratory at Oregon State University, Corvallis.

The main topics to be discussed here are:

1. Fruit and seed development
2. Moisture content of seeds and viscin
3. Seed dormancy and germination
4. Radicle growth
5. Tropistic responses of germinated seeds
6. Influence of light and temperature on infection and subsequent growth of dwarf mistletoe and host trees.

FRUIT AND SEED DEVELOPMENT

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Throughout the decade of the 1970s, we determined the size and weights of fruits and seeds of 6 species of *Arceuthobium* native to Oregon. These measurements were taken in the second year of their maturation, from early June to late August. Selected results are shown in Tables 1 and 2.

Table 1. Developmental increase in fruit and seed size of 6 species of Arceuthobium, 1978.
Each datum based on 30 seeds.

Dwarf mistletoe	Fruit and seed length and width		
	6/14	7/20	7/20
	Fruit (mm)	Fruit (mm)	Seed (mm)
<u>A. abietinum</u>	2.7 x 1.5	4.5 x 2.1	2.4 x 1.2
<u>A. americanum</u>	-- --	4.6 x 2.4	2.0 x 0.9
<u>A. campylopodum</u>	4.0 x 2.0	4.9 x 2.4	2.1 x 1.1
<u>A. douglasii</u>	2.7 x 1.7	4.2 x 2.0	1.8 x 0.9
<u>A. laricis</u>	2.1 x 1.3	-- --	-- --
<u>A. tsugense</u>	-- --	4.0 x 1.7	-- --

Table 2. Developmental increase in fruit size and weight of 4 species of Arceuthobium, 1979.
Each datum based on 30 seeds.

Dwarf mistletoe	Fruit length (mm) and weight (mg)							
	7/25		8/1		8/7		8/16	
	L	Wt	L	Wt	L	Wt	L	Wt
<u>A. abietinum</u>	3.9	11.8	3.5	7.3	3.7	9.7	4.1	12.3
<u>A. americanum</u>	4.0	13.7	4.1	14.3	4.2	15.0	4.6	16.5
<u>A. campylopodum</u>	3.7	10.5	4.6	24.8	5.0	30.0	5.0	28.2
<u>A. douglasii</u>	4.0	8.0	3.5	8.1	3.9	7.6	4.2	9.7

Because seeds are essentially undeveloped in June, the only measurements we could obtain in the early season were of fruit development. Measurements on seed development were not taken until late June.

Fruits showed a fairly uniform dimensional increase throughout the second growing season. Seed size increase followed a sharper gradient than that of fruit size. The rate of seed elongation for all 6 species increased dramatically between mid-July and mid-August. After mid-August, seed elongation nearly ceased, coinciding with a sharp increase in seed weight.

Fruits and seeds varied in size and weight from year to year. For example, seed and fruit weights of fruits and seeds collected in 1972 were smaller than those in 1971, and the seeds constituted a smaller percent of the total fruit weight.

Dwarf mistletoe	Seed wt. as % of fruit wt.	
	1971	1972
<u>A. abietinum</u>	16%	9%
<u>A. americanum</u>	18%	9%
<u>A. campylopodum</u>	14%	9%
<u>A. douglasii</u>	--	10%
<u>A. laricis</u>	--	5%
<u>A. tsugense</u>	16%	8%

In all years, however, seed size approximately doubled in a 30-day period between mid-July and mid-August.

Mature seeds of A. campylopodum were used to determine the relative weights of seeds and viscin. Viscin was removed from seeds with a teasing needle under a dissecting scope, and seeds and viscin were weighed separately. Viscin contributed 26-61% to the combined weight. (Each datum is based on 10 seeds).

Experiment and replicate		Average green weight		
		Total	Seed only	Viscin only
			-- mg --	
1	1	2.0	1.2	0.8 (40%)
	2	2.2	1.6	0.6 (27%)
	3	1.7	1.1	0.6 (35%)
	4	1.9	1.4	0.5 (26%)
2	1	4.3	2.3	2.0 (47%)
	2	4.3	2.3	2.0 (47%)
	3	3.6	1.4	2.2 (61%)
	4	3.1	1.5	1.6 (52%)

MOISTURE CONTENT OF SEEDS AND VISCIN

In studies of A. campylopodum, fresh, mature seeds weighed 2.6-3.0 mg, while seeds dried over drierite weighed 1.6-2.0 mg.

Green seeds	Dried seeds		Basis
	--	Ave. wt. (mg) --	
2.6		2.0	350 seeds
2.7		1.6	70 "
2.7		1.8	250 "
3.0		--	80 "
2.9		--	30 "

In an experiment on fresh seeds of A. campylopodum, the moisture content was determined for 10 batches of 100 seeds each. Moisture content varied from 23% to 47%, with 8 of 10 batches having between 30-45% M.C. Moisture content was calculated by:

$$\frac{\text{green weight} - \text{dried weight}}{\text{green weight}} \times 100$$

The moisture holding capacity was tested for seeds and viscin separately and for intact seeds (each datum based on 10 seeds):

	Seeds without viscin		Viscin only	
	dry	soaked	dry	soaked
	-- mg --	-- mg --	-- mg --	-- mg --
Rep. 1	1.2	2.2	0.8	12.2
2	1.6	2.2	0.6	20.1
3	1.1	2.1	0.5	12.7
4	1.4	2.1	0.5	21.7
Average	1.3	2.2	0.6	16.7

Similar measurements on intact seeds show a weight change from 2.8 mg for fresh seeds, to 21.7 mg for seeds soaked 3 hours in water:

	Fresh seed wt.	Soaked seed wt.
	--mg--	--mg--
Replication 1	2.7	22.7
2	2.4	27.8
3	2.8	34.7
4	3.3	24.7
5	2.5	16.1
6	2.0	20.1
7	3.5	14.9
8	3.2	12.6
Average	2.8 mg	21.7 mg

Clearly the enormous water-holding ability of viscin is an important characteristic of species Arceuthobium, and undoubtedly accounts for their success in areas of low moisture or high evapo-transpiration potential.

We tested the ability of viscin to repeatedly absorb water. Seeds were tested in November, about 3 months after seeds had been harvested and stored at 1.5° C. Fifty seeds (5 replicates of 10 each) were placed on glass, and a similar set placed on filter paper. After 50 wet-dry cycles over 44 days, 26 seeds on filter paper and 16 seeds on glass still swelled normally. At no time was there evidence of irreversible hardening of the viscin. On those seeds which failed to swell after a number of cycles, the viscin appeared to slowly disintegrate, covering progressively less of the seed surface. Even these seeds, however, could be easily moved about the dish when wetted, and they adhered strongly when dried.

In another set of experiments, we recorded weights of A. campylopodum seeds before, during, and after 5 dry-wet cycles. The following tabulation shows the weight of seeds at each weighing (each datum is an average of 20 seeds).

	Experiment 1	Experiment 2
	-- mg --	-- mg --
Initial dry	3.3	3.4
First wet	36.0	32.0
Second dry	3.3	--
Second wet	30.0	20.7
Third dry	3.2	--
Third wet	17.2	17.4
Fourth dry	3.1	--
Fourth wet	--	11.0
Final dry	--	2.7

These data show a loss of viscin per se, and an increasing decline in the ability of viscin to absorb water. The final dry weight is about 85% of the original dry weight, whereas the final wet weight is only about 25% of the original wet weight.

A similar experiment was done comparing the behavior of viscin in 2 Molar solutions of NaCl and glucose.

Cycle	In H ₂ O	In 2M NaCl	In 2M Glucose
		-- mg --	-- mg --
Initial	3.0	2.5	3.1
First wet	46.8	35.6	58.5
Second dry	2.7	5.5	7.6
Second wet	--	--	--
Third dry	--	--	--
Fourth wet	18.1	5.6	26.4
Fourth dry	2.5	2.8	2.6
Fifth wet	9.1	5.0	15.1
Fifth dry	2.4	2.7	2.5
Sixth wet	9.2	4.6	13.4
Sixth dry	2.5	2.8	2.5

Seeds in salt solution absorbed less water than did those in water, but the dry weight of salt-soaked seeds remained higher than the original dry weight. I have no explanation for this, other than it possibly indicates simple osmotic forces. Seeds in glucose solutions absorbed more water than the water controls throughout the experiment. Dry weight of glucose-soaked seeds and the water controls were not different.

Miscellaneous experiments of viscin showed the following:

1. Swollen seeds dropped into boiling water for 5 minutes remained swollen and "normal" looking.
2. Seeds wetted and placed under a lamp at 35° C dried and swelled 12 times with no apparent loss of function.
3. Mistletoe seeds oven dried (104° C) 24 hours had normal swelling response when subsequently placed in water.
4. Viscin on dead seeds absorbed water normally.
5. When fully expanded seeds of A. campylopodum were placed over drierite, the viscin lost 75% of its moisture in 6 hours.

SEED DORMANCY, STORAGE, AND GERMINATION

As with seeds of many other genera, Arceuthobium seeds generally exhibit a post harvest dormancy (Beckman 1964). A. vaginatum is an exception, germinating soon after maturity (Hawksworth 1961). In our studies, seeds of A. campylopodum germinated more quickly with increasing time since seeds were harvested--a phenomenon called "germination readiness" by Beckman (1964). These data from a 1970 test show: (Each germination test utilized 300 seeds (3 replications x 100 seeds)).

Date of harvest	Date of germ. test	Days to max. germ.	Final germ. (%)
9/10	9/30	36-42	16-22
"	10/9	27-33	26-30
"	11/10	17-25	17-24
"	11/19	12-2	22-23
"	12/4	11-18	17-21
"	12/23	5-23	11-26

Another test in 1973 compared germination readiness for two species of Arceuthobium:

Days after harvest	Days to peak germination	<u>A. campylopodum</u>	<u>A. tsugense</u>
8	60	--	--
11	--	35	--
29	45	--	--
51	--	34	--
60	30	--	--
67	--	18	--
90	13	--	--

Germination of seeds of A. campylopodum was better in the light than in the dark under two temperature regimes. (Each datum based on three replications of 50 seeds).

Dwarf mistletoe	10° C		20° C	
	light	dark	light	dark
<u>A. campylopodum</u>	45%	19%	40%	32%
<u>A. tsugense</u>	30%	13%	38%	17%

These data confirm results of Beckman (1964) for A. campylopodum, and by Scharpf and Parmeter (1962) for A. occidentale.

Both Scharpf and Parmeter (1962) and Wicker (1962) state seed germination to be lower than corresponding viability tests using triphenyl tetrazolium chloride (TTC). This suggests that, under optimum conditions, germination could be improved.

RADICLE GROWTH

Radicle growth rates of seeds of A. campylopodum and other species were measured in many experiments over a 10-year period. The following data show rates of radicle elongation per day for 5 regimes: constant low light (350 f.c.) and constant dark--both at 2 temperatures, and a 12-hour light-dark alteration. (Each datum based on 100 seeds).

Temperature	Light	Dark	12hrs, light-dark
10° C	53	24	--
20° C	92	77	45

In contrast, Bonga (1965) reported that light-temperature regimes had no effect on radicle growth of A. pusillum.

Radicle elongation of seeds of A. campylopodum was greater for the first 2 weeks than for the second 2 weeks:

Temperature	Radicle growth per day
10° C	39/day at 14 days 29/day at 34 days
20° C,	75/day at 14 days 59/day at 34 days

Beckman (1964) reported a similar trend of slower growth of older seeds of A. campylopodum.

Age of seeds	Growth/day
0-30 days	196
31-60 "	133
61-90 "	113
91-120 "	23

Radicle elongation of seeds of A. abietinum was determined at 4 temperatures, 32 days after the initiation of germination, and showed best growth elongation at 20° C.

Temperature	Growth/day
15° C	43
20° C	69
25° C	41
30° C	12

The reduction in growth rate past optimum temperature probably reflects the same physiologic stresses (such as high respiration, protein breakdown) that attend any plant that is too warm.

Data reported here are for seeds on glass slides placed in light-boxes within growth chambers and measured periodically with a calibrated dissecting scope. Bonga (1972) noted reduced germination and radicle growth at relative humidities of 90% or below.

An attempt was made to determine the rates of elongation in various combinations of relative humidity and temperature for several species of Arceuthobium. Various relative humidities were developed in flasks over solutions of polyethylene glycol. The growth rates, expressed as micrometers per day are shown for 4 species of Arceuthobium (Table 3).

Table 3. Rates of¹ radicle elongation for 4 species of *Arceuthobium* at 12 temperature-relative humidity regimes.

Relative humidity	<i>A. abietinum</i>			<i>A. campylopodum</i>			<i>A. douglasii</i>			<i>A. tsugense</i>		
	10°	15°	20°	10°	15°	20°	10°	15°	20°	10°	15°	20°
97%	60	68	72	66	64	64	60	--	68	50	62	56
83%	64	--	64	66	--	64	56	--	72	48	--	74
68%	60	--	--	72	--	62	--	--	62	52	--	--
18%	64	--	--	69	--	64	54	--	64	48	--	--

¹The many data-less cells are the result of fungal contamination.

The data show a trend toward greater growth at higher temperatures and higher relative humidity. However, the great variability found in seed performance, and the large number of data-less cells prevent conclusive statements of radicle growth under these experimental conditions.

In our inoculation work, using small seedlings, we found that germinated seeds often fell off, so we tested various adhesives, finding polyvinyl acetate to be best. Comparative tests with *A. campylopodum* seeds with viscin only, and viscin plus polyvinyl acetate, showed that polyvinyl acetate did not influence radicle growth.

Seeds of three species of *Arceuthobium* were "glued" on the edge of upright glass slides and placed in darkened tubes with light from a point source at one end of the tubes. (Each datum based on 50 seeds).

Species	Phototropism		
	negative	positive	neither
<i>A. americanum</i>	90%	0%	10%
<i>A. campylopodum</i>	97%	0%	3%
<i>A. douglasii</i>	81%	0%	19%

Geotropistic responses were determined with similar methods. While the results were less clear-cut, there seemed no pattern of growth that could be interpreted as either negative or positive geotropism:

Species	Radicle growth		
	upward	downward	neither
<i>A. americanum</i>	16%	13%	71%
<i>A. campylopodum</i>	11%	9%	80%
<i>A. douglasii</i>	4%	24%	72%

Efforts to evaluate thigmotropistic responses were not completed, but most species of *Arceuthobium* seem to display a positive thigmotropistic response.

INFLUENCE OF LIGHT AND TEMPERATURE ON INFECTION AND SUBSEQUENT GROWTH OF DWARF MISTLETOE AND HOST TREES

Dwarf mistletoes were called a "light-loving plant" by Weir (1916) because of the rapid development of the epidemic when a stand is partially thinned. In contrast, Wagener (1961) reported that "partial sunlight is more favorable to the establishment of dwarf mistletoe on the host than relatively full or continuous sunshine." Wagener also reported that "robust" dwarf mistletoe development occurred at lower light levels:

Estimated light intensity	% of infections that were "robust"
Strong	2
Good	21
Medium	36
Fair	41

Wagener concluded that "if high light intensity is beneficial to the dwarf mistletoe, it must be exerted indirectly through the effect on the host tree or through the general influence on site conditions."

Our first greenhouse experiments were done with potted seedlings at three levels of shading. In the first experiment, each pot contained one uninfected seedling of ponderosa pine, and one seedling inoculated with germinated seeds of *A. campylopodum*. In the second experiment, pots had one infected pine seedling only. Tree heights, and the number and length of dwarf mistletoe aerial shoots were determined at intervals throughout the duration of the experiments. All pots were given a chill period (5° C, no light) from March to May of 1972, and then returned to the original chamber in the greenhouse. The results are summarized in Table 4.

Table 4. Mistletoe growth response for A. campylopodum on ponderosa pine at 3 levels of shading.

	Level of shading					
	Low shade		Med. shade		High shade	
	Experiment 1	2	Experiment 1	2	Experiment 1	2
Height increase (mm)						
infected seedlings	5	17	10	14	7	10
uninfected seedlings	13	--	14	--	16	--
Increase in number of aerial shoots	50	17	21	4	33	11
Increase in length of aerial shoots (mm)	38	86	79	10	41	45
No. trees that became infected	4/4	4/6	4/4	2/6	4/4	5/6

The greatest number of aerial shoots were produced at the low shade level. The cumulative length of aerial shoots was greatest at low to medium shade, suggesting that mistletoe growth is best at medium or high light levels. Mortality of infected trees was: low shade, 20%; medium shade, 20%; and high shade, 60%. In contrast, no uninfected trees died.

Since this experiment dealt only with levels of light, another study was done in environment chambers, varying both temperature and light. One-hundred and eight ponderosa pine seedlings, each in a 3" plastic pot, were inoculated in April, 1971 with pregerminated seeds of A. campylopodum, and placed in one of three chambers (36 per chamber). Twenty-five were re-inoculated because the seeds died. All three chambers had a 14-hour day, 10-hour night. Night temperatures were 5 degrees below day temperatures. The light and temperature regimes were as follows:

	Light level	Temperature ($^{\circ}$ C)	
	(f.c.)	Day	Night
Chamber #1	1500	25	20
Chamber #2	1500	20	15
Chamber #3	700	25	20

Results of this study are as follows:

Infection

The highest number of seedlings became infected at the low temperature-high light regime (22 of 36 trees). These data agree with Scharpf's report (1969) on the infection rate of Digger pine (Pinus sabiniana) and Monterey pine (P. radiata) by A. occidentale. He reported infection at

constant temperature regimes of 16 and 21 $^{\circ}$ C, but was best at 13 $^{\circ}$ C in an outdoor environment. The high temperature-high light chamber yielded the lowest number of infected plants (13 of 36).

Tree growth

Tree growth was best at high temperature regimes, with the best elongation growth at the low light level for both infected and uninfected trees.

Regime	Height increase	
	Uninfected	Infected
High temp, high light	8 mm	7 mm
High temp, low light	17 mm	13 mm
Low temp, low light	3 mm	3 mm

Also, it appears that the greater the tree growth, the greater the influence of mistletoe on that growth. For example, in the regime most favorable for tree growth, the mistletoe caused the greatest reduction in growth of the infected trees. At the low temperature regime, there was no difference between height growth of infected and uninfected seedlings. Tree height growth was markedly less at low temperatures than at the two high temperature regimes:

	Low temp. High light	High temp. High light	High temp. Low light
	mm	mm	mm
June 1971			
uninfected	17	20	25
infected	16	21	19
Sept. 1971			
uninfected	18	22	39
infected	18	26	30
Jan. 1972			
uninfected	19	29	42
infected	19	26	32

Table 5. Results of tree and dwarf mistletoe growth under 3 temperature-light regimes.

	25-20° C 1500 f.c.	25-20° C 700 f.c.	20-15° C 1500 f.c.
No. trees infected	13 of 36	15 of 36	22 of 36
Total no. aerial shoots after 8 mos.	71	96	81
Mean no. aerial shoots per infected tree	5.5	6.4	3.7
Mean length of longest aerial shoot (mm)	18.4	23.6	13.4
Tree height growth (mm)			
- infected	1.6	2.2	0.9
- uninfected	1.9	3.2	0.9

Aerial Shoots

While low temperature favored infection, high temperature favored mistletoe biomass production. The highest number of aerial shoots were produced at the high temperature-low light regime. This same regime also had the highest average number of aerial shoots per seedling and the longest aerial shoots. (Table 5).

An interesting sidelight was that aerial shoots continued to grow in length after the host trees become dormant. This has also been reported for *A. vaginatum* in the Southwest (Hawsworth 1961). Also, the growth of the aerial shoots corresponded to the growth behavior of the trees: trees which had grown the fastest before the onset of dormancy had the most mistletoe growth after the onset of dormancy. Because dormant trees must be under caretaker status, metabolically speaking, mistletoe growth must reflect the general prosperity of the dormant host tissue, suggesting that the internal nutritional status of the host attained prior to onset of dormancy is important in subsequent mistletoe growth.

Thus, temperature, rather than light, seems to be the main environmental factor influencing mistletoe growth on young seedlings. Better seed survival and infection rate resulted at lower temperature. Subsequent growth of mistletoe was favored by higher temperature. The role of light seems indirect, through its influence on tree processes of photosynthesis, and starch and fat storage.

CONCLUSIONS

Fruit and seed development in species of *Arceuthobium* seem to proceed sequentially: fruit

capsule enlargement, seed elongation, viscin development and, finally, maturation of embryo and endosperm tissue. As shown in Table 2, 60-87% of the final weight of the fruits of 4 species of *Arceuthobium* was attained in the final 22 days of a fruit develops over an approximately 12-month period (Hawsworth and Wiens 1972). Thus, the most energetically costly development occurs immediately prior to maturation. In survival terms, the mistletoe doesn't pay a high cost for fruits lost to environmental hazards, such as predators.

Post-harvest dormancy was present in the species studied in this report. This characteristic reduces survival hazards of a germinated seed exposed to hot fall weather, severe winter cold, and host tissue which is far from succulent. The ability of the seeds to germinate and grow at low temperatures (as early as February) allows infection to occur before the onset of hot summer weather and the appearance of insect predators.

The probability of infection success is increased by the following traits: radicle elongation of 50-100 micrometers per day over a wide range of relative humidities, light intensities, and temperatures; negative phototropism and neutral geotropism (thus, if a seed is on the underside of a limb, it will still be likely to grow upward into host tissue.)

While successful infection seems to be primarily a cool weather event, once organic union with the host is achieved, mistletoe biomass production was greater at higher temperatures. At these higher temperatures, aerial shoot production was greater at lower light levels.

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The Pollination Biology of *Arceuthobium americanum* in Manitoba¹

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Abstract.--There is evidence that both entomophily and anemophily play a significant role in the pollination of *Arceuthobium americanum*. The most commonly trapped insects, a *Bradysia* sp. (Diptera) and *Formica* spp. (Hymenoptera) are thought to be involved in chance pollination of the mistletoe. Among the Coleoptera, *Hyperaspis binotata* (Coccinellidae) and *Cyphon* sp. (Helodidae) were frequently found bearing mistletoe grains on both male and female brooms. Where female brooms were isolated from male brooms only 9% of the insects trapped bore pollen, while 79% of the flowers were pollinated. These data, together with the recovery of airborne pollen at least 400 m from a source, indicate that anemophily is also a significant pollinating mechanism.

INTRODUCTION

The mechanism of pollination in the genus *Arceuthobium*, has been studied since the beginning of the century. A number of floral characteristics suggest entomophily as the mode of pollination, including sessile anthers, spined pollen grains, the clumping of pollen in clusters of 20-40 grains, low pollen production, non-plumose stigma, visual prominence of the male inflorescence and the presence of a glistening stigmatic exudate (Gill and Hawksworth 1961, Player 1979). Additional entomophilous characteristics have been noted by Dowding (1931a) who made reference to the presence of a central cushion in the male flowers of *A. americanum* Nutt. ex Engelm. which bears pairs of glandular cells suggesting nectaries. However, Cohen (1968) in his anatomical study of the staminate flower observed nothing to support this conclusion, although Hawksworth and Wiens (1972) regard the structure as a nectary. Gregor et al. (1974) describe the "pungent, citric-like odor" of both male and female flowers of *A. americanum* which might present olfactory cues to insect visitors. Anthocyanins are found in all species of *Arceuthobium* with dark shoots and in more than half of the light-coloured ones, perhaps functioning as visual attractants to dipteran pollinators (Hawksworth and Wiens 1972). The stigmatic exudate of *A. abietinum* Engelm. was analyzed by Brewer et al. (1974) by thin-layer and gas-liquid chromatography. Flowers produced large (0.24 μ l) droplets of highly concentrated nectar (52-92%) which Brewer

et al. (1974) concluded was probably a strong insect pollinator attractant.

Reports of hymenopterous insects associated with *A. americanum* were made by Weir (1915), and Dowding (1931b) reported both small flies and ants to be the pollinators of *A. americanum*. Kuijt (1955) also observed ants on the male inflorescences of *A. americanum*. Following these observations systematic studies of the insect fauna associated with *Arceuthobium* species were conducted. Stevens and Hawksworth (1970) in a review of the literature concerning the insects and mites associated with dwarf mistletoes concluded that the most common insect pollinator associated with *A. vaginatum* subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens was a thrips of the genus *Frankliniella*, whereas on *A. americanum* small flies such as *Bradysia* sp. (Sciaridae) were common early in the season and succeeded by ants toward the end of the flowering period. The number of possible hymenopteran and dipteran pollinators of *A. americanum* was extended by Gregor et al. (1974) and Penfield et al. (1976) who collected more than 200 insect species bearing *Arceuthobium* pollen, although relatively few species were trapped from mistletoe of both sexes. Only 13 species were considered important and these differed to some extent for each *Arceuthobium* species. The pollinators of *A. americanum* included the ant, *Formica fusca* L. (Formicidae) and the dipterans *Philygria debilis* Lw., *Protophormia terraenovae* (R.-D.) (Calliphoridae), and several *Hylemya* species, *H. ceralis* (Gillette), *H. cinerella* (Faller) and *H. platura* (Meigen) (Anthomyiidae).

Baker (1981) conducted a number of exclusion experiments, using screen bags of 0.8, 2.2 and 4.0 mm mesh and uncovered plants for control, to determine the mode of pollination of *A. pusillum*. Insects were trapped from female witches' brooms,

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on screen traps and sticky board traps. Greater fruit set was recorded on plants covered with 4.0 mm mesh than on branches with smaller screens.

A number of studies to determine the concentrations of airborne mistletoe pollen have been conducted using vaseline-coated microscope slides placed at varying distances from male inflorescences (Gregor et al. 1974, Penfield et al. 1976, Baker 1981). The small number of pollen grains trapped between 2.5 cm and 5 m from male flowers led Gregor et al. (1974) and Baker (1981) to conclude that *A. americanum* and *A. pusillum* were primarily insect pollinated. Penfield et al. (1976) trapped pollen of *A. cyanocarpum* Coulter & Nelson up to much greater distances from the nearest male flowers. While similar quantities of *A. americanum* and *A. cyanocarpum* pollen were trapped over their respective flowering periods, almost five times as much pollen from *A. vaginatum* was trapped. Penfield et al. (1976) concluded that both wind and insects effected pollination but suspected entomophily of being the primary pollinating mechanism.

Player (1979) studied the pollination of *A. douglasii* Engelm. and *A. strictum* Hawksw. & Wigns and found insect visitors were rare to the female flowers of both species. On the other hand laboratory studies indicated that pollen was easily liberated by wind. For continuous trapping of pollen, Player (1977) used square rods which had a higher calculated sampling efficiency at low wind speeds than the theoretical sampling efficiency of microscope slides. However, pollen dispersal was only measured within short distances from male flowers. There was relatively low seed set (2% or less) on female plants screened with mesh 0.5 mm and 1.0 mm in comparison with 11 to 62.5% seed set on uncovered plants. Player concluded that a large component of the wind with its pollen load would likely be forced around the cages. Plants bagged to prevent access of pollen either by insect or wind had no fruit set, ruling out the possibility of apomixis. Player (1979) argued that the pollination of *Arceuthobium* is principally an anemophilous system and based his conclusions on the lack of insect visitors and the relative abundance of airborne pollen.

In Manitoba dwarf mistletoe affects large areas of jack pine and spruce forest, especially in the south of the province in resort areas, where the infected trees are aesthetically displeasing and the dead and dying brooms are a potential fire hazard. A clarification of the pollination mechanism of *Arceuthobium* might be of significance in the development of appropriate control measures. In studies in the United States no specialized and few regular insect visitors have been found, while in Manitoba no systematic observations have been conducted on the insect fauna associated with dwarf mistletoes. Insects were therefore trapped and examined for evidence of pollen to confirm or reject their potential role as vectors.

The majority of studies of airborne pollen concentrations have employed microscope slides coated with petrolatum to form an adhesive surface. The levels of airborne *Arceuthobium* pollen measured with this method have been low. Moreover, most

dwarf mistletoe pollen trapped on slides has been in the immediate vicinity of male flowers while reports of long distance travel of pollen have been rare. In the present study concentrations of airborne dwarf mistletoe pollen and medium distance transfer were investigated using cheesecloth traps.

METHODS AND MATERIALS

A. Insects

Insects were trapped from dwarf mistletoe brooms using a beat net and kill jars for three consecutive seasons 1981 - 1983.

In 1981 three sites were chosen so that insects could be sampled from different environments:

1. Exposed lakeshore.
2. Sheltered, closed forest
3. Open forest

At each site, insects were trapped from female and male brooms at three times, morning (10.00 a.m. to 12.00 noon), noon (12.00 noon to 2.00 p.m.), and afternoon (2.00 p.m. to 4.00 p.m.), during the course of three days, in May, 1981. In 1981, 155 brooms were sampled; 86 male and 69 female.

A preliminary analysis indicated that the numbers of insects trapped by site, day and time of sampling were not significantly different, whereas a significant difference existed between the numbers of insects trapped from male and female brooms. Insects bearing pollen and trapped from female brooms were of most interest in the study, therefore in 1982 more female than male brooms were sampled, 73 female as opposed to 30 male. Insects were sampled from the three sites on 5 days in May, 1982.

Within the forest, where male and female brooms were in close proximity, insects with pollen adhering to them were trapped from brooms of both sexes. To identify pollen-bearing insects that might seek and pollinate female plants of *A. americanum*, five young jack pines with female dwarf mistletoe infections that were situated at least 10 m from the nearest male infection were sampled in the final season. Insects were trapped at weekly intervals from the start of the flowering period (April 26) until the male flowers dehisced, at the end of May.

B. Wind

In 1982 and 1983 cheesecloth traps were used to collect airborne pollen. Cheesecloth was stretched over a square wire frame 15 x 15 cm and supported by 2 m bamboo poles. A 9 x 9 cm square from the centre of each trap was later scanned under a dissecting microscope for evidence of airborne mistletoe pollen. Sizes of pollen clusters and total numbers of grains per trap were recorded.

In 1982 two sites were chosen where stands of dwarf mistletoe-infected jack pine flanked areas which had been clear cut. Traps (3 replicates) were erected at 25 m, 50 m, and 100 m, from the pollen source. The cheesecloth was replaced six times at 24-hour intervals and twice at 4-day intervals. Before the male flowers opened in 1983, traps were erected 100 m, 200 m, 300 m, and 400 m from the pollen source at two similar sites. The cheesecloth traps were examined at the end of the seven week pollination period, June 7, 1983.

In 1983 five young jack pines bearing female dwarf mistletoe brooms established in a clear cut area were selected and marked. Two traps were erected by each tree on April 19, 1983 and changed at weekly intervals for the duration of the flowering period. Insects were trapped at weekly intervals from the same trees. At the start of the pollination period the number of developing fruits on 5 mistletoe plants on each tree plus one control tree from which insects were not trapped, were counted. In August, 1983, the same plants were examined to determine the number of flowers fertilized in the spring of 1983.

RESULTS AND DISCUSSION

A. Insects

A preliminary list of the insects trapped from A. americanum is given in Table 1. The four orders Diptera, Hymenoptera, Coleoptera and Hemiptera comprised almost 95% of the insects trapped. Thysanopterans were found relatively frequently (28, 5.7%) in 1981, four of which had a single grain adhering to them. Only one was found in 1982 and none in 1983. In 1981 three of the trapped insects belonged to the order Homoptera, in 1982 none and in 1983 two. Two microlepidopterans were trapped in both 1982 and 1983. These orders, Thysanoptera, Homoptera, and Microlepidoptera have been omitted from further analysis on account of their scarcity.

In 1981 and 1983 insects of the orders Diptera and Hymenoptera were trapped most frequently (Figs. 1, 3) while the orders Hymenoptera and Coleoptera were represented more frequently in 1982 (Fig. 2). In all three seasons the majority of the dipterans were Bradysia sp. (Scleridae) (1981, 55%; 1982, 36%; and 1983, 54%) whereas Formicidae, Formica spp. (fusca and rufa groups) and Tapinoma sessile, comprised most of the Hymenoptera (1981, 70%; 1982, 61%; and 1983, 48%). The coccinellid, Hyperaspis binotata was especially abundant at Site 2 in 1981 and comprised 38% of all the coleopterans trapped in that year. Other insect taxa included in the list of insects associated with A. americanum were isolated less frequently.

In both years more than 50% of all the insects trapped from male and female brooms combined bore at least one pollen grain, although the majority of pollen bearing insects were trapped from male brooms (Table 2). Of the insects trapped on male brooms in 1981 and 1982,

Table 1. Preliminary list of insects collected from brooms of Pinus banksiana induced by Arceuthobium americanum in Belair Provincial Forest, Manitoba, 1981-1983.

			1981	1982	1983
DIPTERA	UNIDENTIFIED	6 specimens	-	+	-
	CECIDOMYIIDAE	2 specimens	-	-	+
	CHIRONOMIDAE	2 specimens	-	-	+
	CHLOROPIDAE	1 specimen	+	-	-
	EPHYRIDAE	3 specimens	-	-	+
		<u>Phlygria debilis</u> Lw.	+	+	+
		<u>Psilopsa olga</u> Cresson	+	+	-
	MUSCIDAE	<u>Musca domestica</u> L.	+	-	-
	MYCETOPHILIDAE	1 specimen	-	-	+
	SCIARIDAE	<u>Bradysia</u> sp.	+	+	+
		<u>Corynoptera</u> sp.	+	-	-
		<u>Lycoriella</u> sp.	+	-	-
	TEPHRI- TIDAE	<u>Tephritis</u> sp. <u>araneosa</u> (Coquil- let)?	+	-	-
	HYMEN- OPTERA	UNIDENTIFIED	15 specimens	-	+
	CHALCIDOIDEA	3 specimens	+	-	+
COLEOPTERA	CHALCIDIDAE	1 specimen	-	-	+
	ENCYRTIDAE	1 specimen	+	-	-
	PTEROMALIDAE	5 specimens	+	+	+
	BRACONIDAE	3 specimens	+	-	+
	FORMICIDAE	<u>Camponotus herculeanus</u> (Linne)	+	-	-
		<u>Dolichoderus taschenbergi</u> (Mayr)	+	-	-
		<u>Formica</u> sp., <u>fusca</u> group	+	+	+
		<u>Lasius sitkaensis</u> Pergande	+	-	-
		<u>Tapinoma sessile</u> (Say)	-	-	+
	SCELIONIDAE	1 specimen	+	-	-
	TENTHREDINIDAE	2 specimens	-	+	+
	XYELIDAE	1 specimen	+	-	-
	UNIDENTIFIED	5 specimens	-	+	+
	BUPRESTI- DAE	<u>Chrysobothris</u> sp.	+	-	-
	CHRYSO- MELIDAE	<u>Calligrapha</u> sp.	-	+	-
HEMIPTERA	COCCIN- ELLIDAE	<u>Coccinella</u> sp.	-	+	-
		<u>Coccinella transversoguttata</u> Fald.	-	+	+
		<u>Hippodamia tridecimpunctata</u> (L.)	+	+	-
		<u>Hyperaspis binotata</u> Say	+	-	-
		<u>Mulsantina hudsonica</u> Casey	+	-	-
		<u>Scymnus</u> (<u>Pullus</u>) <u>lacustris</u> Lec.	+	+	-
	CURCULIONIDAE	1 specimen	+	-	-
	ELATERIDAE	<u>Ctenicera triundulatus</u> (Rand.)	+	+	+
	HELODIDAE	<u>Cyphon</u> sp.	-	+	+
	LATHRIDII- DAE	<u>Corticaria</u> sp.	+	+	-
	MELYRIDAE	<u>Amecocerus</u> sp.	+	+	-
	LYGAEIDAE	<u>Kleidocerys resedae</u> (Parzer)	+	+	-
		<u>Ischnorrhynchus</u> sp.	-	+	-
		<u>Nysius ericae</u> (Schilling)	-	+	-
	MIRIDAE	<u>Lygus</u> sp.	-	-	+
HOMOPTERA	CICADELLI- DAE	1 specimen	-	-	+
	PSYLLIDAE	<u>Trioza obtusa</u> Patch	+	-	-
		<u>T. tripunctata</u> (Fitch)	+	-	-
MICROLEPIDOPTERA UNIDENTIFIED			-	+	+
THYSANOPTERA UNIDENTIFIED			+	+	-

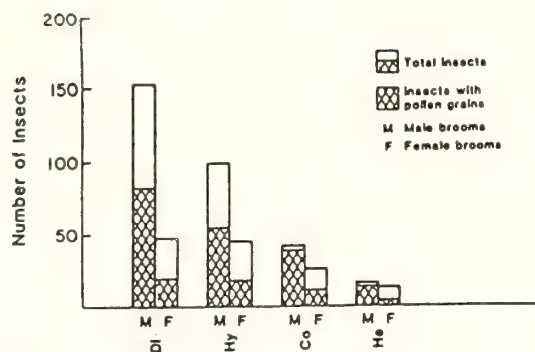


Fig. 1. Diptera, Hymenoptera, Coleoptera, and Hemiptera trapped from brooms of *Pinus banksiana* induced by 86 male and 69 female infections of *Arceuthobium americanum* in Belair Provincial Forest, Manitoba, 1981.

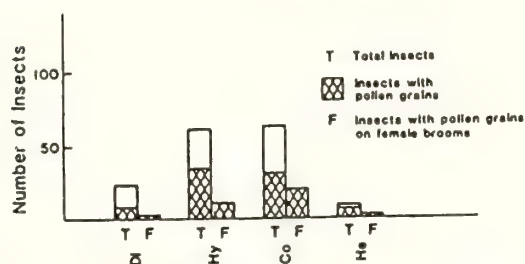


Fig. 2. Diptera, Hymenoptera, Coleoptera, and Hemiptera trapped from brooms of *Pinus banksiana* induced by 30 male and 73 female infections of *Arceuthobium americanum* in Belair Provincial Forest, Manitoba, 1981.

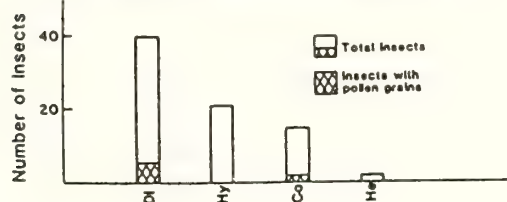


Fig. 3. Diptera, Hymenoptera, Coleoptera, and Hemiptera trapped from five brooms of *Pinus banksiana* induced by female *Arceuthobium americanum* in Belair Provincial Forest, Manitoba, at six weekly intervals in 1983.

Table 2. Percentage of insects bearing mistle-toe pollen from brooms of *Pinus banksiana* induced by *Arceuthobium americanum* in Belair Provincial Forest, Manitoba.

YEAR	NUMBER OF BROOMS		MEAN NUMBER OF INSECTS PER BROOM		% INSECTS WITH POLLEN	
	M	F	M	F	M	F
1981	86	69	3.7	2.4	60	34
1982	30	73	2.0	1.4	72	39
1983		30		2.7		9

60% and 72% respectively carried pollen, whereas for the same seasons, 34% and 39% respectively of insects trapped on female brooms bore pollen (Table 2). In 1983 the number of pollen-bearing insects trapped on female brooms was considerably lower, 9% (Table 2), than in either 1981 or 1982. Fewer brooms were sampled in 1983 but the mean number of insects per broom was 2.6, which was comparable to the numbers collected in 1981.

Several of the insect families collected in Manitoba were represented in earlier studies in the United States. Of the Diptera, Mycetophilidae (Fungus gnats; one specimen trapped), was the only family not previously associated with *A. americanum* (Gregor et al. 1974, Penfield et al. 1976). The majority of the Diptera trapped belonged to families characterized by sucking mouthparts (Cecidomyiidae, Chironomidae, Ephydriidae, Mycetophilidae and Sciaridae). The small fly *Bradysia* sp. (Sciaridae) was collected most frequently from both male and female brooms in Manitoba and was commonly well dusted with pollen. Sciaridae has been described as the chief anthophilous dipteran family (Proctor and Yeo 1972).

The families Braconidae, Encyrtidae, Pteromalidae, Scelionidae, and Tenthredinidae (Hymenoptera) were poorly represented in the Manitoba study, but have been found in association with *A. americanum* in Utah or Colorado (Gregor et al. 1974; Penfield et al. 1976). The super-family, Chalcidoidea and family Chalcididae plus the family Xyelidae are reported in this association for the first time. Chalcid wasps have been recorded at flowers (Proctor and Yeo 1972), and larvae of the Xyelidae are known to feed on the staminate cones of pines (Rose and Lindquist 1973). However, the family in the Hymenoptera best represented was the Formicidae. Ants regularly collect nectar from flowers but are unlikely to effect cross-pollination as the workers responsible for nectar collection, are wingless and have to reach flowers by crawling up the trunks of trees and stems of flowers (Proctor and Yeo 1972). Several genera (*Lasius*, *Camponotus*, *Formica*) and two species (*Formica* sp. *fusca* group, *Tapinoma sessile*) have been trapped in the United States as well as in Canada. Many ants were found covered with *A. americanum* pollen or with it clustered about the mouthparts, but pollen was not observed on ants trapped from female dwarf mistletoe that was isolated from male infections in 1983 (Fig. 3).

Among the Coleoptera, Coccinellidae, Elateridae and Melyridae were collected in both the United States and Canada; the Melyridae is the one exclusively anthophilous family among this group (Proctor and Yeo 1972). Many specimens of *Ctenicera triundulatus* (Elateridae) were found with abundant pollen adhering to them, but the family is known to feed destructively on flowers, offsetting the value of any chance pollination effected by the damage they cause (Proctor and Yeo 1972). Different species of the genera *Ctenicera* (Elateridae), *Mulsantina* and *Scymnus* (Coccinellidae) have been reported from both Colorado and Utah, United States and from Manitoba, Canada. *Coccinella transversoguttata* represents the one coleopteran species that is presently known as a denizen of *A. americanum*.

infected pine both in the United States (Utah) and Manitoba. As a family the Coccinellidae are primarily an entomophagous group but nectar and pollen also commonly provide an alternate food source when insect food is scarce, permitting survival and immediate resumption of oviposition when insect prey reappear (Hagen 1962, Hodek 1973). Ladybird beetles (Coccinellidae) were not considered important pollinators of dwarf mistletoe by Gregor et al. (1974) or Penfield et al. (1976); however, *Hyperaspis binotata* was one of the most common insect visitors to *A. americanum* in Manitoba, and pollen grains were frequently found about the mouthparts and adhering to the ventral surface. The marsh beetle, *Cyphon* sp. (Helodidae) was also frequently found on brooms and well dusted with pollen in the final two years of the study.

Kleidocerys resedae was the only hemipteran recorded with any frequency from *A. americanum* in Manitoba; the family (Lygaeidae) and genus have not been recorded in this association elsewhere. Members of this order have often been recorded at other flowers (Proctor and Yeo 1972). The piercing sucking mouthparts suck up the juices of the plants but the bugs may become dusted with pollen and effect chance pollination as they move from flower to flower (Proctor and Yeo 1972). *K. resedae*, well dusted with pollen, were trapped from both male and female brooms from Site 1 in 1981 (Fig. 1).

A number of insects reported as anthophilous and implicated in the pollination of flowers were found in the immediate vicinity of *A. americanum* in Belair Provincial Forest. While the majority of insects, including those that were well dusted with pollen, were trapped on male brooms, a significant number were taken from female brooms that were in close proximity to male brooms (Figs. 1, 2). However, insects with pollen were rarely trapped from female brooms that were isolated from male brooms (Fig. 3).

B. Wind

Total pollen counts and number of clusters of pollen (dispersal units) trapped at 25 m, 50 m, and 100 m from the source (1982) varied greatly, but with no consistent pattern, between sites, ranging from 0 to 60 for total pollen count per 24 hour period and 0 to 18 for number of dispersal units over a similar interval of time (Table 3). Considerable variation between sites and traps was also observed in 1983 (Table 4). However, analysis of variance to determine the effect of site and distance revealed that the number of pollen grains and dispersal units trapped at each distance did not vary significantly between the two sites in 1982 so the data were combined. Although the numbers of dispersal units (each of which can only effect the pollination of a single female flower) were found to increase slightly with distance from the source, the concentration of airborne pollen was relatively uniform over the distance measured. However, the percentage of single pollen grains was greater at 50 m and 100 m (Fig. 4). At 25 m, 64% of the dispersal units were single grains whereas at 50 m and 100 m 79% and 71% respectively were single grains. An ANOVA to determine the effect

of site and distance on the number of pollen grains trapped at 100 m to 400 m in 1983 revealed that significantly more pollen was trapped from site 1, exposed to sources both to the north and east, than at site 2 where pollen was dispersed from the east alone. Significantly more pollen clusters were trapped at 200 m and 300 m at both sites, although the highest percentage, 73%, of single pollen grains occurred in traps farthest from the source (Fig. 5). Smaller clusters are expected as distance increases but their numbers may also have risen as a result of the disintegration of dispersal units. From 100 m to 300 m the percentage of single grains was lower, ranging from 24-35% (Fig. 5).

Airborne pollen of *A. americanum* was found at greater distances from the source than might have been expected from previous studies (Gregor et al. 1974, Baker 1981). Player (1979) did not measure pollen dispersal beyond 7 m but Gregor et al. (1974) found no *A. americanum* pollen more than 1 m from source. Baker (1981) concluded that the numbers of airborne pollen grains of *A. pusillum* ($0.4/\text{cm}^2/\text{year}$) trapped within 5 m of male flowers were too low to support the hypothesis of an anemophilous pollination mechanism. Penfield et al. (1976), however, trapped pollen of *A. cyanocarpum* up to 151 m from the nearest male flowers.

Higher numbers of dispersal units were trapped in 1982 in a two week period, in which sampling was conducted at several 24-hour intervals and two 4-day intervals, than in 1983 when the traps were exposed for the entire pollination period (Figs. 4, 5). A possible explanation of the disparity in the pollen counts between 1982 and 1983 is the washing of pollen from the traps by rain during the course of the seven week exposure.

Dips and peaks were observed in the concentration of airborne pollen in 1982 and 1983 suggesting that release is not uniform or continuous over the pollination period. The climatic data available failed to implicate either temperature or precipitation as the sole cause for arrest or retardation of pollen discharge. However, the sites were close to Lake Winnipeg, a large body of water which would no doubt influence local temperature and precipitation, while the study had to rely on the climatic records of Environment Canada Meteorological Office for Pine Falls, the closest meteorological station to the study sites and some 16 km distant. This may have obscured the relationship between airborne pollen concentrations and temperature and/or precipitation.

POLLINATION SUCCESS

The experiment to determine the number of successfully pollinated flowers on trees isolated from male dwarf mistletoe infections was disturbed in a number of ways. Several tags were chewed, presumably by rodents, and several stems of mistletoe either eaten or dislodged. Some tags were chewed through and had fallen off making it impossible to make the second count on several plants. One entire tree and several tagged plants had died from other causes. Only 14 of the original twenty-five marked plants on the experimental trees and one of the five

Table 3. Total counts of pollen grains and dispersal units of *Arceuthobium americanum* recorded for Sites 1 and 2 at increasing distances from the source in Belair Provincial Forest, Manitoba, 12-25 May, 1982.

Date May 1983	Total Pollen Count*							Dispersal Units*					
	25 m		50 m		100 m		Total	25 m		50 m		100 m	
	Site		Site		Site			Site		Site		Site	
	1	2	1	2	1	2		1	2	1	2	1	2
12	0	34	26	4	9	1	74	0	3	2	4	4	1
13	10	0	2	12	0	60	84	1	0	2	3	0	1
14	3	11	4	7	4	2	31	3	10	4	7	4	2
15-18	9	56	33	50	50	51	249	8	34	16	45	35	43
19	3	2	0	1	0	2	8	3	2	0	1	0	2
20	20	14	13	36	11	19	113	4	9	5	15	6	16
21	10	11	4	8	53	21	107	5	6	3	8	18	12
22-25	184	61	89	63	249	88	734	65	30	52	34	56	25
Totals	239	189	171	181	376	244		89	94	84	118	123	102
Mean number per trap	80	63	57	60	125	81		30	31	28	39	41	34

* Sum of 3 replicates.

Table 4. Total counts of pollen grains and dispersal units of *Arceuthobium americanum* recorded for Sites 1 and 2 at increasing distances from the source in Belair Provincial Forest, Manitoba, 19 April to 7 June, 1983.

	100 m		200 m		300 m		400 m	
	Site		Site		Site		Site	
	1	2	1	2	1	2	1	2
Total pollen count *	13	17	48	41	59	37	10	6
Dispersal units *	5	11	4	15	15	18	9	5

* Count for one trap

on the control tree (from which no insect collection was attempted) remained at the time of the second count (Table 5). On the 15 surviving plants just 50% of the developing fruits counted in April reached maturity. Considerably more flowers appeared to have been pollinated in the spring of 1983 (272) than 1982 (99) (Table 5), although a count made in the spring of 1984 revealed that only 12%, 20 out of 172 developing fruits that were traced, had overwintered successfully. The reason for such low survival requires further study.

GENERAL DISCUSSION

There is evidence that both entomophily and anemophily play a role in the pollination of *A. americanum*.

Members of several anthophilous insect families some well dusted with pollen, were found associated with dwarf mistletoe flowers. Ants of the genus *Formica* and *Bradysia* sp. (Scleridae) have commonly been reported as insect pollinators of *A. americanum* in earlier studies (Gregor et al. 1974, Penfield et al. 1976). In Manitoba, two coleopterans, *Hyperaspis binotata* (Coccinellidae) and *Cyphon* sp. (Helodidae), were frequently trapped and may effect a degree of pollination. However, the scarcity of *H. binotata* after 1981 and the absence of *Cyphon* sp. in the first year of sampling is perhaps indicative of a local and erratic population buildup in some insect species. Presumably, flowers such as *A. americanum* with no special adaptations to specific insect pollinators are placed at advantage if such a population explosion occurs in a pollinating insect species. None of the insects reported showed specific adaptations for the pollination of *A. americanum*; rather it would appear that a number of unspecialized insect visitors are responsible for chance pollen transfer in conjunction with nectar and/or pollen predation. However, in 1983 insects bearing pollen and trapped from female *A. americanum* isolated from male brooms were few, 9% of the total, although an appreciable percentage, 79%, of flowers with receptive stigmata were fertilized. The experiment had been disturbed, but the pollination success was high, suggesting that the wind as a pollination mechanism of *A. americanum* was effective.

Pollen was trapped up to 400 m from the source over a clear cut area which provides evidence that, in spite of its entomophilous characteristics, presence of spines and tendency to cluster, it is easily transported by the wind. At approximately 20 μ diam., *A. americanum* pollen falls within the

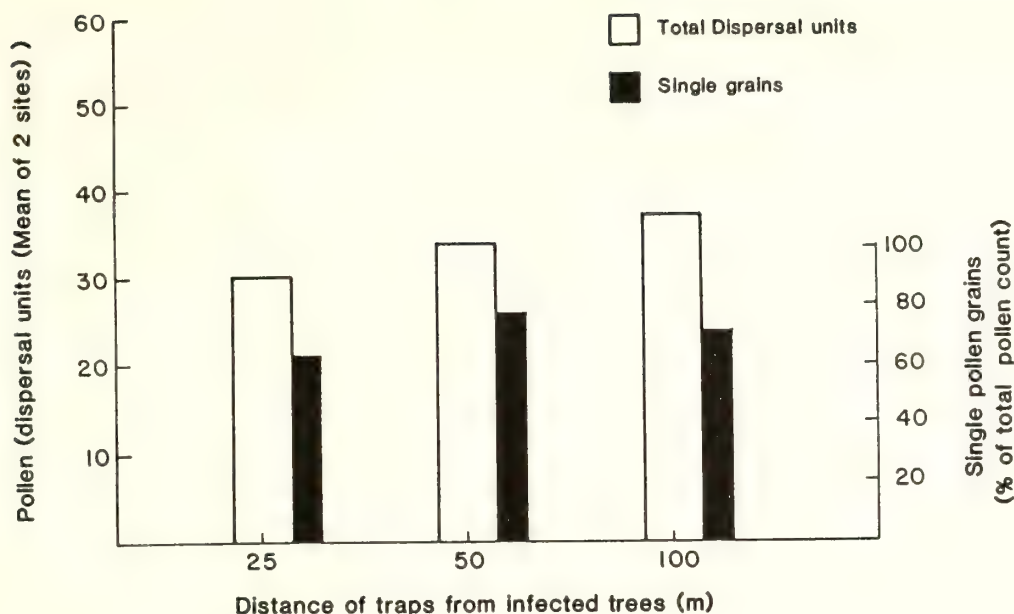


Fig. 4. Dispersal of *Arceuthobium americanum* pollen in Belair Provincial Forest, Manitoba, 1982.

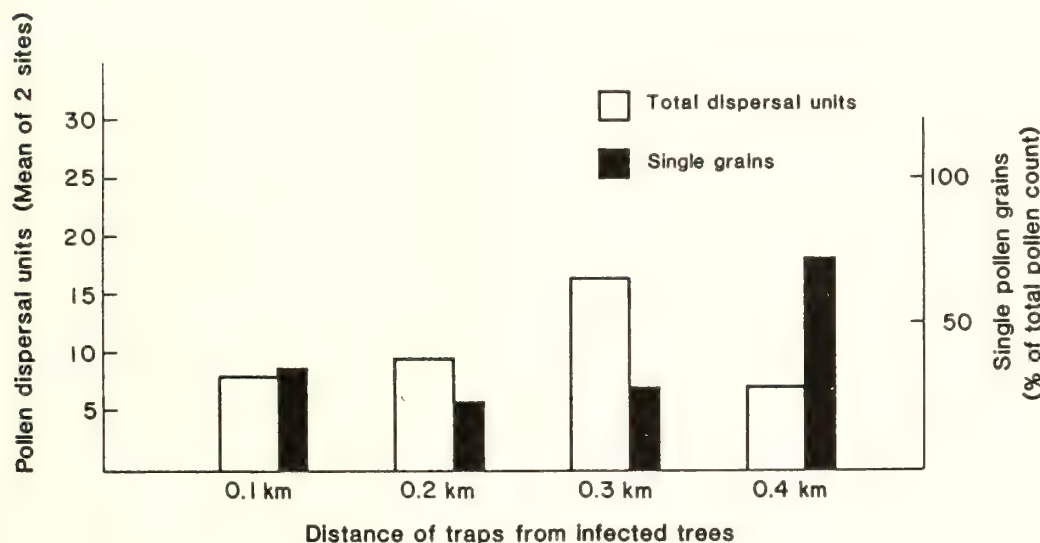


Fig. 5. Dispersal of *Arceuthobium americanum* pollen in Belair Provincial Forest, Manitoba, 1983.

size range encountered in most wind-pollinated species (Whitehead 1969).

EFFICIENCY OF TRAPPING AIRBORNE POLLEN

Most studies have concluded that both insects and wind are effective pollinators of *A. americanum*; opinions differ as to which is the primary mechanism (Baker 1981, Gregor et al. 1974, Penfield et al. 1976, Player 1979). Microscope slides, coated with vaseline or petrolatum, have been commonly used to

trap airborne spores and pollen and were employed by the supporters of entomophily (Baker 1981, Gregor et al. 1974, Penfield et al. 1976). However, microscope slides have poor theoretical collection efficiency at the low wind speeds observed within a forest, 0.0% at 1 m/sec and 46% at 10 m/sec (Player 1979). The problem is exacerbated when the spores in question are small (Gregory 1973), and it is most probable that the method has led to an underestimation of the airborne pollen load.

Table 5. Pollination success of tagged plants of female Arceuthobium americanum infected Pinus banksiana isolated from male infections in Belair Provincial Forest, 1983.

Tree	Plant	First count (April 1983)	Second count (August 1983)		Third count (June 1984)
		Developing fruits	Mature fruits	Developing fruits	Mature fruits
1	1	2	0	32	*
	2	0	0	15	—
	3	0	0	43	0
	4	0	0	24	2
	5	0	0	6	0
3	1	3	0	13	8
	2	18	2	1	0
	3	7	2	1	0
	4	0	0	2	0
	5	4	1	2	0
4	1	1	1	0	0
5	2	45	35	31	—
	3	0	0	68	0
	5	19	11	22	—
CONTROL	2	0	0	12	10
TOTALS	15	99	50	272	20

* Tags lost over winter.

The cheesecloth traps used in the present study avoided some of the problems associated with sticky slides. Air passes through the cloth trapping a proportion of the spined pollen grains on the cheesecloth fibers. The pollen grains of A. americanum are small (20 μ) and probably carried in the airstream around a microscope slide unless the wind speed is high enough to give momentum sufficient for impaction of the spores. While the cheesecloth traps can only give an indication of the relative concentrations of pollen in the air it is felt that they may give a better estimation than the microscope slides.

In conclusion, there is sufficient evidence to suggest that both entomophily and anemophily are important pollination mechanisms of A. americanum depending on the local environment in which pollen transfer is taking place. Anemophily is most likely to be of significance in open forest and for medium distance transfer of pollen while within closed forest chance visits by unspecialized insect visitors will effect a degree of pollination; that is, "some plants make the best of both worlds" (Gregory 1973).

An experiment was conducted in the spring of 1984 to compare the relative efficiency of the cheesecloth traps used in this study with greased microscope slides. The data have yet to be analysed and no conclusions can be drawn at this time.

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Insect-Dwarf Mistletoe Associations: an Update¹

Robert E. Stevens and Frank G. Hawksworth²

Abstract.--The last 10 years have seen a marked increase in the attention given insect-dwarf mistletoe relationships. Areas of interest include insects as pollinators, insects phytophagous on dwarf mistletoe shoots, flowers, and seeds, and combined insect-dwarf mistletoe effects in tree mortality. The latter category has been the subject of considerable work in the area of increased susceptibility of dwarf mistletoe-infected trees to bark beetles, especially Dendroctonus. Many insects of dwarf mistletoes have been identified but much more research will be needed before their potential as practical biological control agents can be assessed.

In 1970, we reviewed arthropod-dwarf mistletoe relationships (Stevens and Hawksworth 1970), and identified 3 general kinds of associations between insects and dwarf mistletoes: (1) pollination of dwarf mistletoe by insects, (2) insects feeding on dwarf mistletoe, and (3) increased tree susceptibility to insect attack induced by dwarf mistletoe. The pertinent literature up to the mid-1970's was reviewed by Scharpf (1975).

The 1970s saw a marked increase in attention given to these associations, and it seems useful at this time to update our treatment of them. The 3 categories of relationships are still pertinent.

INSECTS AS POLLINATORS OF DWARF MISTLETOES

In our earlier paper (Stevens and Hawksworth 1970), we noted that a variety of thrips, bees, ants, and flies had been reported to participate in dwarf mistletoe pollination. We speculated about the possibility of limiting pollination and dwarf mistletoe spread by controlling or repelling arthropod pollinators.

Since our 1970 paper, several studies (Gregor et al. 1974, Penfield et al. 1976, and Player 1979), have significantly broadened our knowledge about dwarf mistletoe pollination ecology, and several others have added important details (see Gilbert and Punter, these proceedings).

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In the earliest of the major studies, Gregor et al. (1974), observed at least 25 species of insects on flowers of Arceuthobium americanum on Pinus contorta in Utah. Flies (Anthomyiidae, Syrphidae, Calliphoridae, Muscidae, and Ephydriidae), and ants (Formicidae), were the most common insect visitors. The authors felt that the evidence pointed toward pollination by insects (entomophily) being more important than that by wind (anemophily).

In the Colorado study by Penfield et al. (1976), over 200 species of insects were found bearing pollen of A. americanum, A. vaginatum, and A. cyanocarpum. However, the authors also acknowledged that wind was also likely an important element in pollination, with some pollen being dispersed up to 150 meters from its source. In this paper it was felt that ants and flies were the most important insect pollinators. The ubiquitous thrips (considered important by some workers) while numerous, were found to remain excessively long on male dwarf mistletoe flowers, arriving on female inflorescences too late to be effective in pollination.

Player (1979), conducting studies in the Douglas-fir forests of Utah (A. douglasii) and pine forests of northern Mexico (A. strictum), did not find an extensive entomofauna involved in pollination, particularly in the case of A. douglasii. He opted for anemophily as the general pollination mechanism in Arceuthobium.

In an unpublished report, Williams (1970) found unidentified thrips common on flowers of A. campylopodum infecting P. jeffreyi in San Diego County, California. Williams discusses more thrips activity in male than female flowers, which may be significant in light of the findings by Penfield et al. (1976).

Baker et al. (1978) briefly report studying the role of wind and insects in pollination of A. pusillum in Minnesota. A large fly and a

beetle, both unidentified, "were found to carry large amounts of pollen." The authors considered wind pollination to be of minor importance.

In summary, there does not appear to be a clear case for either anemophily or entomophily. It seems likely both are involved. Given all this, limiting pollination via insect control and thus limiting dwarf mistletoe spread seems an unlikely prospect.

INSECTS FEEDING ON DWARF MISTLETOES

In Stevens and Hawksworth (1970), we listed a variety of kinds of insects that fed on dwarf mistletoes. Advances in this area since 1970 in the United States have mostly been limited to additional reports of occurrences of known species, and descriptions of species associated with dwarf mistletoe. However, the period also saw several U.S. Department of Agriculture-supported studies in Pakistan aimed at basic understanding of dwarf mistletoe-insect relationships on the Indian subcontinent.

Larvae of Mitoura (Callophrys) spinetorum are well-known as herbivores on dwarf mistletoe, and the adults are prized by butterfly collectors. According to Ferris and Brown (1981), the species "occupies a wide distribution throughout the western United States." Other recent reports of its occurrence are found in Austin (1981), Emmel and Emmel (1973), Holland (1974), Kohler (1980), Tilden and Huntinger (1977), and Tunnock and Dooling (1976).

Tietz (1972) repeats an earlier report of M. johnsoni (McCorkle 1962); however, he errs in calling the host A. douglasii. The main host of M. johnsoni is A. tsugense. We (Stevens and Hawksworth 1970) overlooked McCorkle (1962). Evidently M. johnsoni has a 1-year life cycle, and the larvae feed readily on A. tsugense and sometimes on other species of Arceuthobium. McCorkle (in Anonymous 1982) noted that, in an Oregon study, 28 larvae of M. johnsoni completely destroyed 106 of 144 A. tsugense shoots.

Another lycaenid butterfly, Lycaenopsis cinerea Edwards, was reported for the first time feeding on A. americanum in British Columbia (Ross et al. 1973).

Spittlebugs, often seen on dwarf mistletoe in the southwestern United States, were the subject of several reports in the 1970's and early 1980's (Fuller and Hostetler 1980, Lessard 1978, Lessard and Walters 1978, and Ragenovich 1980). In our earlier paper (Stevens and Hawksworth 1970), we commented on the nomenclature of the species reported to be on dwarf mistletoe, Clastoptera obtusa (Say). Specimens from a recent (1978) collection in Arizona were authoritatively identified as C. distincta Doering; we now presume that the citations of C. obtusa as a dwarf mistletoe associate were errors.

The work in Pakistan, conducted during the period 1973-1976 (Baloch and Ghani 1980), was an initial search for insects feeding on A. minutissimum and A. oxycedri, with an eye toward biological control. Cosmotola inops Prout, a geometrid, was the sole species found feeding on A. minutissimum. This insect has a 1-year life cycle, overwintering as 3rd and 4th instars. Two species of moths, Diorctria taiella Amsel (Pyralidae), and Prosinitis florivora Meyrick (Blastobasidae), fed on A. oxycedri. Both species overwinter as larvae, and are univoltine. Other insects recorded from A. oxycedri (Baloch et al. 1977), include Polydrusus obligatus Fst. and Systates sp. (Coleoptera, Curculionidae); Dolycoris indicus Stal. (Hemiptera, Pentatomidae); and Dichrocytus valesianus (Hemiptera, Miridae). Nothing more is reported of this latter set.

In Colorado, Stevens et al. (1977) found larvae of a normally pine-feeding tortricid moth, Choristoneura lambertiana ponderosana Obraztsov, colonizing A. vaginatum. Late-stage larvae fed heavily on the dwarf mistletoe, and apparently normal, though smaller, moths were produced. Emergence of the moths that fed on dwarf mistletoe was delayed about 2 weeks.

Several new insect associates have been described from dwarf mistletoe since 1970. All but a thrips, Frankliniella hawksworthii O'Neill, which may be a pollinator, are presumed to feed on dwarf mistletoe shoots or flowers. These newly-described species and some described species first reported on Arceuthobium are listed in Table 1.

In a somewhat unusual context, Hawksworth and Wicker (1973) for the first time reported the common Aspidiotus nerii (Bouché) (Homoptera, Coccidae), as a dwarf mistletoe associate. This species and Hemiberlesia rapax (Comstock), both colonizing A. hondurensis, were infected with Nectria flammiae (Tulasne) Dingley, a common parasite of scale insects, in Honduras.

Another insect-dwarf mistletoe relationship that has received little attention, but is may be significant in the mistletoe's life history is insect predation of seeds before and after germination. In inoculation studies with A. vaginatum in ponderosa pine in Arizona, nearly 70% of the planted seeds were removed or destroyed, mostly by undetermined insects (Hawksworth 1961). Insects are also involved in seed predation of A. tsugense in Oregon (Carpenter et al. 1979) and of several species of dwarf mistletoe in the Inland Empire (Wicker 1967). Studies to determine the insects involved in dwarf mistletoe seed predation are needed.

INCREASED TREE SUSCEPTIBILITY TO
INSECTS INDUCED BY DWARF MISTLETOE

A major recent development in the understanding of the ecology of forest insects-- particularly bark beetles (Scolytidae)-- and

diseases has been the increasing awareness that these kinds of pest organisms often act together in causing tree mortality. Typically, pest complexes--involving both bark beetles and diseases--are the causes of tree death. The California Pest Damage Inventory has done much to clarify the complex interactions of insects, diseases, and environment in tree mortality (Byler 1978, Smith and Roettgering 1982).

The increase in the number of publications on this kind of association between insects and dwarf mistletoe shows the interest in the topic. When we completed our review 14 years ago (Stevens and Hawksworth 1970), we cited only 10 references. Today there are more than 100. Many of these publications report observational material only, but a few report quantitative data. Some of the most significant reports on association of dwarf mistletoes and insects in relation to tree mortality are summarized in Table 2.

The nature of the association between "primary" bark beetles (*Dendroctonus*) and dwarf mistletoes is still poorly understood. Many variables, including the host, locality, and environmental factors, influence the association. In some cases, the prevailing evidence is that dwarf mistletoe increases susceptibility to the insects (e.g., *Dendroctonus ponderosae* and *D. brevicornis* in ponderosa pine) but, in other instances, there seems to be little or no effect (e.g., *D. pseudotsugae* in *Pseudotsuga menziesii*), and in others, dwarf mistletoe-infested trees may be less susceptible (e.g., *D. ponderosae* in *Pinus contorta*). There are many reports and observations that "secondary" insect

species (*Ips*, *Melanophila*, etc.) attack mistletoe-weakened trees and hasten their death.

Twig beetles frequently infest and kill mistletoe-infected branches. Some specific records provided by Malcolm Furniss (personal communication 1982) are as follows: (1) *Pityophthorus schwartzii* Blackman on ponderosa pine infected by *Arceuthobium vaginatum* on the Coronado National Forest Arizona, and (2) *Pityophthorus deletus* Le Conte on limber pine infected by *Arceuthobium cyanocarpum* on the Dixie National Forest, Utah.

DISCUSSION

Where can we look for added understanding of insect-dwarf mistletoe relationships, and where can these help in forest management? It would appear that pollination ecology is complex enough so that simple solutions to mistletoe spread will not come easily from this approach.

We have shown that several phytophagous insect species have been identified as likely biological control agents. Additional work on this management approach surely appears justified.

Finally, as forest management becomes more intensive in western North America, further attention to bark beetle-dwarf mistletoe relationships may provide clues to potential problem areas. It is encouraging to note that more and more foresters are viewing these pest problems as often complex, and not always resulting from actions of a single kind of organism.

Table 1. Species of insects newly reported to feed on dwarf mistletoes, 1970-1984

Insect	Host	Tree	Locality	Reference
THYSANOPTERA				
Thripidae				
<i>Frankliniella hawksworthii</i> O'Neil	<i>A. vaginatum</i>	<i>Pinus ponderosa</i>	Colorado	O'Neill 1970
HEMIPTERA				
Miridae				
<i>Neoborella canadensis</i> Kelton & Herring	<i>A. americanum</i>	<i>Pinus banksiana</i>	Alberta, Canada	Kelton & Herring 1978
<i>N. pseudotsugae</i> Kelton & Herring	<i>A. douglasii</i>	<i>Pseudotsuga menziesii</i>	Arizona, and New Mexico	Kelton & Herring 1978
<i>N. xanthenes</i> Herring	<i>A. americanum</i>	<i>Pinus contorta</i>	Colorado	Herring 1972
<i>Platylagus mexicanus</i> Kelton	"mistletoe" ¹	<i>Pinus leiophylla</i>	Durango, Mexico	Kelton & Knight 1970
COLEOPTERA				
Scolytidae				
<i>Pityophthorus arceuthobii</i> Wood	<i>A. globosum</i>	<i>Pinus montezuma</i>	Durango, Mexico	Wood 1971
Mordellidae				
Unidentified morellid	<i>A. abietinum</i>	<i>Abies magnifica</i>	California	R. F. Scharpf, Personal Communication, 1983
ORTHOPTERA				
Locustodea				
<i>Malanoplus devastator</i> Scudder	<i>A. campylopodum</i>	<i>Pinus ponderosa</i>	California	R. F. Scharpf, Personal Communication, 1984

¹ Probably is *A. gillii* subsp. *nigrum* (F.G.H.).

Table 2. Reports and observations of dwarf mistletoe-insect associations in relation to tree mortality, 1970-1984.

Host and location	Insect and dwarf mistletoe association	Reference
<u>Abies spp.</u>		
California	Eighty percent of the mortality in red and white fir was due to a 3-organism complex, <u>Scolytus ventralis</u> , <u>Fomes annosus</u> , and dwarf mistletoe.	California Forest Pest Control Action Council, 1975
California	Dwarf mistletoe is a secondary cause of death in red and white fir; it weakens trees to the point that insects are attracted in sufficient numbers to kill them.	Gordon 1973
<u>Pinus banksiana</u>		
Manitoba	The pine wood nematode, <u>Bursaphelenchus xylophilus</u> was found in trees declining because of dwarf mistletoe infestation.	Burnes et al. 1983
<u>Pinus contorta</u>		
Rocky Mountains	<u>Dendroctonus ponderosae</u> . The beetles' strong preference for preference for trees of large diameters make it difficult to separate the influence of dwarf mistletoe from that of diameter.	Amman 1978
Colorado	<u>Dendroctonus ponderosae</u> and dwarf mistletoe were associated in all areas evaluated on the White River National Forest.	Lister 1973
Colorado	<u>Dendroctonus ponderosae</u> . In a study of over 1,000 trees little correlation was found between phloem thickness and intensity of dwarf mistletoe infestation.	Hawksworth et al. 1983
Northern Rockies	<u>Dendroctonus ponderosae</u> losses are less in heavy mistletoe-infested stands, probably because of thinner phloem in mistletoe-infected trees. However, an exception is for local bole infections where the thicker bark makes them more likely to be hit by the beetle.	McGregor 1978
Idaho	<u>Dendroctonus ponderosae</u> killed many trees weakened by dwarf mistletoe. In two of three areas studied, beetle losses were more than twice as high in heavily-infested as in healthy or lightly-infested stands.	Parker and Stipe 1974
Idaho	<u>Dendroctonus ponderosae</u> is less likely to attack mistletoe-infected trees because they have thinner phloem - an average of 0.12 inches for diseased trees, and 0.17 inches for healthy trees.	Roe and Amman 1970
General	Interactions of <u>Dendroctonus ponderosae</u> and dwarf mistletoe are complex, and related mostly to ecological status of the stands. Openings caused by mountain pine beetle tend to intensify dwarf mistletoe in the residual stands.	Wellner 1978
Oregon	Large trees that survive <u>Dendroctonus ponderosae</u> epidemics have significantly higher levels of dwarf mistletoe than smaller, less beetle-susceptible trees.	Ziegler 1978
<u>Pinus edulis</u>		
Colorado	<u>Ips</u> sp. and dwarf mistletoe associated with dying pinyon in Mesa Verde National Park.	James and Lister 1978
<u>Pinus jeffreyi</u>		
California	In the Laguna Mountains in southern California pines weakened by dwarf mistletoe are attacked and killed by the California flathead borer, <u>Melanophila californica</u> .	Swain 1972, Swain et al. 1974 Wood et al. 1979
California	In the San Bernardino National Forest an insect-disease complex was responsible for 68% of the tree mortality. The complex consists of 4 insects, 3 fungi, and dwarf mistletoe.	Smith and Roettgering 1982
<u>Pinus ponderosa</u>		
California	About 1/3 of the trees killed in the central Sierra Nevadas died from a combination of bark beetles and diseases (including dwarf mistletoe).	California Forest Pest Control Action Council 1975
California	Losses due to bark beetles and dwarf mistletoe were greatly accelerated during the drought years 1977-1978.	Page 1981

Table 2. Reports and observations of dwarf mistletoe-insect associations in relation to tree mortality, 1970-1984.

Host and location	Insect and dwarf mistletoe association	Reference
California	All but 1 of about 200 mistletoe-infected trees killed in campgrounds died from a combination of causes: dwarf mistletoe and insects (bark beetles, engraver beetles, and flathead borers).	Vogler and Scharpf 1981
Arizona	<u>Coloradia pandora</u> . Trees heavily attacked by dwarf mistletoe are more readily killed pandora moth defoliation than lightly- or un-infected trees.	M. Wagner and R. E. Mathiasen, Personal Communication, 1984
Arizona, New Mexico	<u>Ips lecontei</u> . Trees weakened by dwarf mistletoe favor Ips beetle buildup.	Parker 1979
New Mexico	<u>Dendroctonus adjunctus</u> . In three areas studied in the Lincoln National Forest, mortality due to the roundheaded pine beetle was directly related to intensity of dwarf mistletoe infection.	Stevens and Flake 1974
New Mexico	<u>Dendroctonus adjunctus</u> , <u>D. parallecolus</u> , and <u>Ips</u> sp. Found a direct relationships between dwarf mistletoe intensity and bark beetle attack.	Parker et al. 1975
Colorado	<u>Dendroctonus ponderosae</u> . Mountain pine beetle show definite preference for mistletoe-infected trees. Eighty-two % of the beetle killed trees had dwarf mistletoe.	Frye and Landis 1975
Colorado	<u>Dendroctonus ponderosae</u> . Found no association between the bark beetle and dwarf mistletoe where the disease is light, but there may be a strong attraction of the beetle to heavily infected trees.	Johnson et al. 1976
Colorado	<u>Dendroctonus ponderosae</u> . Mountain pine beetle broods and attack density were not significantly different in healthy and heavily mistletoe-infected trees.	McCambridge 1980
Colorado	<u>Dendroctonus ponderosae</u> . Nearly 70% of the trees assumed to have been killed by mountain pine beetle also were attacked by Armillaria root disease and/or dwarf mistletoe.	Fuller, L. R. 1983
Colorado	<u>Dendroctonus ponderosae</u> . In an area in northern Colorado, 31% of the mistletoe-infected trees, but only 20% of the non-mistletoed trees, were killed by the mountain pine beetle.	McCambridge et al. 1982
<u>Pinus radiata</u>		
California	Dwarf mistletoe-infected trees are commonly prone to bark beetle attack.	Old 1979
<u>Pinus</u> spp.		
Guatemala	<u>Dendroctonus frontinalis</u> . Bark beetles are most severe in trees attacked by dwarf mistletoe and a resinous canker.	Anonymous 1973
<u>Pseudotsuga menziesii</u>		
Idaho	<u>Dendroctonus pseudotsugae</u> . No correlation was observed between susceptibility to Douglas-fir beetle and intensity of dwarf mistletoe.	Furniss et al. 1981
California, Arizona	<u>Melanophila drummondi</u> . Trees weakened by Douglas fir dwarf mistletoe are attacked and killed by this borer.	USDA Forest Service 1978; Furniss & Hawksworth, unpublished observations
<u>Juniperus excelsa</u>		
Pakistan	Several species of wood borers are associated with killing junipers infected by dwarf mistletoe.	Chaudrhy and Wali-ur-Rehmin 1979

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Animal Vectors of Dwarf Mistletoe, with Special Reference to *Arceuthobium americanum* on Lodgepole Pine¹

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Abstract.--This paper summarizes studies of animal vectors of dwarf mistletoes with special reference to *Arceuthobium americanum* on lodgepole pine in Colorado. A total of 23 vectors has been identified. Results show birds can inoculate susceptible trees and that establishment of dwarf mistletoes beyond the range of their explosive fruits can be explained by vector dissemination of seed.

INTRODUCTION

Dwarf mistletoes, *Arceuthobium* spp., are parasitic plants which are regarded as one of the most damaging disease agents of conifers in the United States. An estimated 418 million cubic feet of wood fiber are lost annually because of these pathogens either through growth reduction or tree mortality (Drummond 1982). Dwarf mistletoes also adversely affect wood quality, while reducing cone and seed production in infected trees. An understanding of how dwarf mistletoes are spread is critical to their effective control. Local seed dispersal of dwarf mistletoes via their explosive fruits has been studied in detail (Hinds and Hawksworth 1965), but little is known about the long-range dispersal of *Arceuthobium* spp. The establishment of dwarf mistletoe infections beyond the range of their explosive fruits indicates involvement of vectors and shows the need for further research on this subject. This paper summarizes the evidence currently available on the importance of animal vectors in the spread of dwarf mistletoes, and describes recent research on vectors of *Arceuthobium americanum* in lodgepole pine (*Pinus contorta*) in Colorado.

LITERATURE REVIEW

Long-distance dissemination of dwarf mistletoes has been a subject of much speculation, but until recently, little definitive research. Isolated pockets of dwarf mistletoe infection have been found beyond the normal range of explosive fruits (table 1). Hawksworth and Weins (1972) reported numerous cases of *A. pusillum* on islands off the Maine Coast and in Lake Michigan. Hawksworth et al. (1975) found *A. cyanocarpum* on ponderosa pine (*P. ponderosa*) 8 km from the nearest infection source, thus suspecting local seed dispersal by birds. Buckland and Marples (1952) believed that scattered *A. campylopodum* infections in regenerated stands of western hemlock (*Tsuga heterophylla*) in British Columbia were initiated by animal or bird activity. Mathiasen (1979), in a survey of the lower peninsula of Michigan, found that *A. pusillum* infected less than one percent of the black spruce stands but occurred in widely scattered infection centers that may have originated from bird-disseminated mistletoe seed. Urban (1968) reported the occurrence of several isolated infection centers of *A. cyanocarpum* in limber pine (*P. flexilis*) stands of Craters of the Moon National Monument, Idaho. He observed that birds and rodents may have been accountable for these infections, which contributed to the distribution and spread of the parasite within the hosts' range. Hudler and Hawksworth (1979), in a study of *A. vaginatum* subsp. *cryptopodum* on ponderosa pine in Colorado, found 32 satellite infection centers ranging in size from one tree to 0.3 ha in a study area of 340 ha. They concluded that some agent, probably birds, was responsible for the occurrence of the infection centers as far as 450 m from the nearest potential seed source.

Anderson (1949) observed that gray jays (*Perisoreus canadensis*), chickadees (*Parus* spp.) and nuthatches (*Sitta* spp.) may have been responsible for establishing numerous isolated

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responsible for establishing numerous isolated infections of A. pusillum in black spruce (Picea mariana) stands in Minnesota. He speculated that seeds could adhere to birds searching for food and that these seeds could later be transferred to healthy trees. In black spruce stands in Minnesota, Ostry (1978) found 12 A. pusillum satellite infection centers that were too far from main infection centers to have originated from explosively disseminated seed. The satellite infection centers ranged in size from a single infected tree to a center 30 by 52 m containing more than 100 infected trees. The centers were located 72 to 736 m away from the main infection center and 30 to 250 m away from the other nearest satellite infection centers. Ostry determined that these satellite infection centers were not remnants of the previous stand but resulted from vector-borne seed.

Hawksworth, Nicholls, and Merrill (unpublished data), in a study of A. americanum on lodgepole pine in Colorado, found 25 isolated infection centers in an area of about 15 ha that appeared to have originated from vector-disseminated mistletoe seed. Isolated pockets of A. douglasii on Douglas-fir (Pseudotsuga menziesii) and A. abietinum on white fir (Abies concolor) were found on the south rim of the Grand Canyon in Arizona. The nearest source of the parasite was 16 km away on the north rim of the Canyon (Hawksworth 1967).

The recent discoveries of isolated populations of A. abietinum in Arizona and

Table 1.--Possible vector initiated dwarf mistletoe sites based upon the literature through 1983.

<u>Arceuthobium</u> species	Location	Reference
<u>A. douglasii</u>	Arizona	Hawksworth 1967
<u>A. abietinum</u>	Arizona	Hawksworth 1967
<u>A. abietinum</u>	Arizona	Mathiasen et al. 1983
<u>A. microcarpum</u>	Arizona	Mathiasen et al. 1983
<u>A. campylopodum</u>	British Columbia	Buckland and Marples 1952
<u>A. cyanocarpum</u>	Colorado	Hawksworth et al. 1975
<u>A. vaginatum</u>	Colorado	Hudler and Hawksworth 1979
<u>A. americanum</u>	Colorado	Authors' obser- vations 1982-83
<u>A. cyanocarpum</u>	Idaho	Urban 1968
<u>A. pusillum</u>	Maine	Hawksworth and Weins 1972
<u>A. pusillum</u>	Michigan	Hawksworth and Weins 1972
<u>A. pusillum</u>	Michigan	Mathiasen 1979
<u>A. pusillum</u>	Minnesota	Anderson 1949
<u>A. pusillum</u>	Minnesota	Ostry 1978

A. microcarpum in New Mexico 270 to 400 km beyond their previously known ranges suggest that long-distance bird dispersal may have been involved (Mathiasen and Jones 1983).

Dwarf mistletoe infections are frequently found in the tops of trees where birds tend to spend time watching and preening (figs. 1A and B). The tops of conifers are highly susceptible because of the high proportion of young susceptible tissues and, once infected, the tops have a greater potential for establishing new infections in surrounding trees (Zilka and Tinnin 1976).

These examples, and others, provide strong circumstantial evidence that vectors are involved in the dissemination of dwarf mistletoe seed and explain the origin of pockets of infection found far from main infection centers. These kind of observations have stimulated studies designed to identify vectors of Arceuthobium spp. in order to fill a major gap in the understanding of dwarf mistletoe life histories (table 2). A summary of research on vectors of dwarf mistletoe follows.

Hudler et al. (1974) found seeds of A. pusillum of black spruce on gray jays and a red squirrel (Tamiasciurus hudsonicus) in a Minnesota study. In some instances, seeds of A. pusillum were known to be carried as far as 100 m by gray jays.

Ostry et al. (1983), in a Minnesota study of A. pusillum on black spruce, captured a total of 250 birds and squirrels representing 45 species. In 2 years of trapping during dwarf mistletoe seed dispersal, they found that 28 animals of seven species had a total of 45 seeds on their bodies. During a peak seed dispersal period in 1974, they found seeds on 12 percent (N=58) of the birds and squirrels captured and, in 1975, they found seeds on 20 percent (N=64) of the animals captured. Animals found with seed were the gray jay, yellow warbler (Dendroica petechia), palm warbler (Dendroica palmarum), yellow-rumped warbler (Dendroica coronata), dark-eyed junco (Junco hyemalis), red squirrel, and flying squirrel (Glaucomys sabrinus). Because of the difficulty of observing animals actually inoculating trees in the field, Ostry et al. (1983) set up controlled experiments in which dwarf mistletoe seeds were placed on captive birds who were observed in cages with potted black spruce. Birds were observed removing some of the seeds during preening. Several of the removed seeds stuck to susceptible portions of trees, providing the first conclusive evidence that birds can inoculate trees. Presumably this is what also occurs under field conditions, according to the authors.

Singh (1982) found that A. pusillum is one of the principal agents damaging black spruce on the island of Newfoundland, where it causes up to 86-percent tree infection and up to 37-percent tree mortality. The patchy distribution of the parasite matched sites inhabited by the

Newfoundland gray jay (Perisoreus canadensis sanfordi), some of which harbored dwarf mistletoe seeds.

Zilka and Tinnin (1976) studied bird-dwarf mistletoe relationships in the Pacific Northwest. During a brief collection period in the fall of 1973, 18 birds representing 11 species were collected. Four birds, Cassin's finch (Carpodacus cassinii), mountain chickadee (Parus gambeli), red crossbill (Loxia curvirostra), and Steller's jay (Cyanocitta stelleri) carried seeds on their feathers. The authors reported that the Steller's jay is particularly important as a potential vector because it often spends time in the highest perches of a tree watching and preening. In addition, most of the species they observed frequently chose brooms for night perches where they would easily be hit by dispersing seed. The authors reported 28 instances, in 350 hrs of observation, of birds being struck by seeds.



Figure 1A.--Gray jay on a typical preening or watching perch at the top of a host tree.



Figure 1B.--Dwarf mistletoe infection typical of those from vector-disseminated seed, on top of a Douglas fir tree.

Table 2.--Number of dwarf mistletoe vector species identified by various investigators.

No. vector species identified	Location	Mistletoe in study area	Reference
4	Oregon	6 <u>Arceuthobium</u> spp.	Zilka and Tinnin 1976
1	Oregon	4 <u>Arceuthobium</u> spp.	Lemons 1978
2	Minnesota	<u>Arceuthobium pusillum</u>	Hudler et al. 1974
7	Minnesota	<u>Arceuthobium pusillum</u>	Ostry et al. 1983
1	Newfoundland	<u>Arceuthobium pusillum</u>	Singh 1982
5	Colorado	<u>Arceuthobium vaginatum</u>	Hudler and Hawksworth 1979
14	Colorado	<u>Arceuthobium americanum</u>	Authors' observations 1982-83

Many bird species use mosses and foliose lichens for nesting materials that also serve as an excellent reservoir for viable dwarf mistletoe seeds. Zilka and Tinnin (1976) reported finding seeds in five of seven nests observed; these seeds could constitute an important source of inoculum in regrowth of clear-cut areas. They also identified 10 avian species where frequency of occurrence and behavior imply a significant role in seed transport.

Hudler and Hawksworth (1979) conducted studies in a Colorado ponderosa pine forest infested with A. vaginatum subsp. cryptopodum. A total of 411 birds representing 21 species were trapped, with 4 percent carrying dwarf mistletoe seed. These birds included the pygmy nuthatch (Sitta pygmaea), mountain chickadee, gray-headed junco (Junco caniceps), chipping sparrow (Spizella passerina), and Williamson's sapsucker (Sphyrapicus thyroideus). On eight occasions they observed mountain chickadees to be struck by discharging seeds which adhered to their feathers as was the case with pygmy nuthatches on six occasions. In five instances, chickadees hit by discharged seeds continued foraging in tips of ponderosa pine branches, and seeds were transferred from birds to pine needles. These observations confirmed that birds can inoculate susceptible trees in the field.

Lemons (1978) investigated the role that small mammals play in dwarf mistletoe seed dispersal in the Malheur National Forest in Oregon. Arceuthobium spp. present were A. campylopodum, A. douglasii, A. laricis and A. americanum, and the primary host species of each were Pinus ponderosa, Pseudotsuga menziesii, Larix occidentalis and Pinus contorta,

respectively. Two study areas were established. Red squirrels were examined in each area when the seeds began to disperse. No seeds were found on squirrels where infection was low, but 50 percent of the squirrels trapped or shot in a more heavily infected area carried seeds on their fur. Lemons thought that squirrels carried mistletoe seed over distances up to 150 m, but doubted that many infections resulted because most seeds carried on the fur were probably groomed off in an uninfected part of the host tree.

Another association that may lead to mistletoe seed vectoring is the establishment of nests by birds and mammals in dwarf mistletoe-caused witches' brooms (Tinnin et al. 1982; Weir 1916). Some records and observations of such nestings are given in table 3. Although, in general, most nesting activities are completed before late summer-early fall mistletoe seed dispersal, late nesting by some species overlaps the seed dispersal period.

Based on the results of foregoing studies, 23 bird and mammal vectors have been identified (table 4). Vectors of dwarf mistletoe may be

Table 3.--Reports of birds and mammals nesting in Arceuthobium-caused witches' brooms.

Animal	Location	Reference
BIRDS		
Pine Siskin (<u>Carduelis pinus</u>)	Oregon	Zilka 1973
Gray Jay (<u>Perisoreus canadensis</u>)	Minnesota	Warren 1899
Red Crossbill (<u>Loxia curvirostra</u>)	Colorado	Bailey et al. 1953
Robin (<u>Turdus migratorius</u>)	Colorado	Authors' observation
House Wren (<u>Troglodytes aedon</u>)	Arizona	Authors' observation
Spotted Owl (<u>Strix occidentalis</u>)	New Mexico	Lignon 1926
	Oregon	Forsman 1983
Accipiter Hawks (<u>Accipiter spp.</u>)	Oregon	Reynolds et al. 1982
MAMMALS		
Red Squirrel (<u>Tamiasciurus hudsonicus</u>)	Minnesota	Ostry 1978
	Colorado	Hatt 1943
Abert Squirrel (<u>Sciurus aberti</u>)	Colorado	Farentinos 1972

Table 4.--Identified vectors of dwarf mistletoe based upon the literature through 1983.

Birds	Mammals
Gray Jay (<u>Perisoreus canadensis</u>)	Red Squirrel (<u>Tamiasciurus hudsonicus</u>)
Steller's Jay (<u>Cyanocitta stelleri</u>)	Flying Squirrel (<u>Glaucomys sabrinus</u>)
Three-toed Woodpecker (<u>Picoides tridactylus</u>)	Golden-mantled Squirrel (<u>Citellus lateralis</u>)
Williamson's Sapsucker (<u>Sphyrapicus thyroideus</u>)	Pine Marten (<u>Martes americana</u>)
Robin (<u>Turdus migratorius</u>)	Least Chipmunk (<u>Eutamias minimus</u>)
Dark-eyed Junco (<u>Junco hyemalis</u>)	
Gray-headed Junco (<u>Junco caniceps</u>)	
Hermit Thrush (<u>Catharus guttatus</u>)	
N. Saw-whet Owl (<u>Aegolius acadicus</u>)	
Yellow Warbler (<u>Dendroica petechia</u>)	
Palm Warbler (<u>Dendroica palmarum</u>)	
Yellow-rumped Warbler (<u>Dendroica coronata</u>)	
Mountain Chickadee (<u>Parus gambeli</u>)	
Cassin's Finch (<u>Carpodacus cassinii</u>)	
Pygmy Nuthatch (<u>Sitta pygmaea</u>)	
Chipping Sparrow (<u>Spizella passerina</u>)	
Townsend's Solitaire (<u>Myadestes townsendi</u>)	
Red Crossbill (<u>Loxia curvirostra</u>)	

more important in the short-and long-range distribution of dwarf mistletoe than originally thought. Even though animal dissemination and resulting infection may be infrequent, this probable means of seed dispersal enables dwarf mistletoe to become established and to spread in new locations. These new infection centers may hinder otherwise effective silvicultural control measures.

LODGEPOLE PINE DWARF MISTLETOE STUDY

To gain more insight into dwarf mistletoe-vector biology, we conducted a study to identify vectors of lodgepole pine dwarf mistletoe in Colorado and to determine their potential importance in the establishment of new infection centers.

METHODS

Our study was conducted in 1982-1983 during *A. americanum* seed dispersal on the Fraser Experimental Forest in the Arapaho National Forest near Winter Park, Colorado. The lodgepole pine forest is mainly *Abies lasiocarpa/Vaccinium scoparium* habitat type. Birds and mammals were trapped in lodgepole pine stands using cell traps and mist nets up to 445 m in total length (fig. 2). Trapped animals were examined; and the number and location of seeds adhering to their bodies were observed and recorded (fig. 3). The seeds were removed and some were tested for viability by immersing them in 0.2 percent W/V aqueous 2, 3, 5-triphenyl tetrazolium chloride (TTC) for 24 to 48 hr. The viable seed endosperm stained pink while nonviable seeds remained unstained (Scharpf 1970). Birds were then banded and mammals were ear-tagged so that individuals could be identified upon recapture. Movements of animals within the study area were monitored by retrapping, color marking, or radio telemetry (fig. 4).

Timing of dwarf mistletoe seed dispersal throughout August and September was monitored by making daily seed counts on cloth seed traps placed on the ground near infected trees. These seeds were also checked for viability using the TTC chemical test. The distribution of satellite infection centers on the study area was determined by surveying for the presence or absence of dwarf mistletoe on 1,450 plots taken at 1-chain intervals in a 60-ha area.



Figure 2.--Steller's jay caught in a mist net used to trap birds.



Figure 3.--Examining a Steller's jay carefully for mistletoe seed or, Steller's jay examining pathologist for seeds.



Figure 4.--Gray jay with a 3.5 g radio transmitter used to follow its movements between dwarf mistletoe infected and healthy lodgepole pine stands.

RESULTS

Ten bird (table 5) and four mammal (table 6) species were identified as potential vectors of dwarf mistletoe. A total of 626 birds (including retraps = IRT) of 30 species and 300 mammals (IRT) of four species was trapped and examined for seed. For the entire study period, 7 percent of the birds and 9 percent of the mammals carried

seed (table 7). A total of 84 seeds was found on 71 animals during this period (44 on birds and 27 on mammals). During a 16-day peak seed-dispersal period in 1982, 22 percent of the birds (N = 55 IRT) and 20 percent of the mammals (N = 80 IRT) had seed. The most important vectors were the gray jay, Steller's jay (fig. 5), mountain chickadee, and least chipmunk (Eutamias minimus) (fig 6).

Five gray jays were radio-tracked in 1983, verifying that the birds frequently moved back and forth between infected and healthy stands of lodgepole pine. Some of the radioed birds were known to be carrying seed at the time they were radio-tracked. Color-marked birds provided similar information. Telemetry studies of five gray jays showed that their home ranges covered 21 to 51 ha.

None of the birds were observed eating mistletoe seed. They acquired seed, however, when foraging for food in infected trees as seeds were being explosively discharged from dwarf mistletoe fruits. The seeds, sticky with viscin, easily stuck to feathers. Most seeds were found on lower body parts around legs, on the breast, and under wings and tail. Of 20 seeds removed from animals and tested with TTC, 65 percent were viable.

Both resident and migratory birds were captured with seeds on their feathers. This indicates that seeds could be disseminated over short distances by resident birds and over long distances by migratory birds.

Table 5.--Bird vectors of lodgepole pine dwarf mistletoe trapped on the Fraser Experimental Forest in Colorado during 1982-1983.

Species	1982		1983 -	
	No. Trap- ped	% with seed	No. Trap- ped	% with seed
Steller's Jay (<u>Cyanocitta stelleri</u>)	10	30	14	7
Gray Jay (<u>Perisoreus canadensis</u>)	41	24	74	15
Three-Toed Woodpecker (<u>Picoides tridactylus</u>)	8	13	1	0
Mt. Chickadee (<u>Parus gambeli</u>)	23	9	52	6
Y.-Rumped Warbler (<u>Dendroica coronata</u>)	57	5	9	0
Robin (<u>Turdus migratorius</u>)	21	5	11	9
G.-Headed Junco (<u>Junco caniceps</u>)	39	3	62	3
Hermit Thrush (<u>Catharus guttatus</u>)	33	3	39	3
Townsend's Solitaire (<u>Myadestes townsendi</u>)	1	0	2	50
N. Saw-whet Owl (<u>Aegolius acadicus</u>)	4	0	5	40

Table 6.--Mammal vectors of lodgepole pine dwarf mistletoe trapped on the Fraser Experimental Forest in Colorado during 1982-1983.

Species	1982		1983	
	No. Trap- ped	% with seed	No. Trap- ped	% with seed
Least Chipmunk (<u>Eutamias minimus</u>)	78	19	187	4
G.-mantled Squirrel (<u>Citellus lateralis</u>)	17	12	3	33
Pine Marten (<u>Martes americana</u>)	1	100	0	0
Red Squirrel (<u>Tamiasciurus hudsonicus</u>)	0	0	9	11

Table 7.--Summary of vectors of lodgepole pine dwarf mistletoe, Fraser Experimental Forest, Colorado, 1982-1983.

Animal	No. trapped	No. with seed	% with seed
Birds	626	44	7
Mammals	300	27	9
Totals	926 ¹	71 ²	$\bar{X} = 7.2$

¹Includes retrapped animals.

²A total of 84 seeds was found on these 71 animals.

One mammal, a least chipmunk, was seen feeding on dwarf mistletoe berries for about 20 minutes. In the process, it ended up with at least five seeds on its fur. Least chipmunks spent most of their time on the ground where they inadvertently picked up seeds already released from berries. This was also true for the golden-mantled squirrel (Citellus lateralis). In contrast, red squirrels also spent time in trees cutting down cones and storing mushrooms in dwarf mistletoe brooms and other branches. They were frequently observed brushing against mistletoe shoots during these activities. The home ranges of these mammals were small and appeared to be important only in local dwarf mistletoe dissemination and intensification.

During the 1983 study period, a total of 966 seeds was counted on seed traps at three different elevations. TTC tests revealed that 65 percent of a sample of these seeds (N = 66) were viable. Beginning the week of August 15, dispersal progressed from the lowest elevation to highest elevation over a period of 6 weeks (fig. 7). This increased the time of potential seed contact for migratory birds and resident birds that had the same kind of elevation differences in their home range as did the gray and Steller's

jays. Because of this longer seed dispersal period, there were more opportunities for these birds to come in contact with seeds than in infected stands with little elevational differences and a corresponding shorter seed dispersal period.

A total of 1,450 plots (established at 20-m grids) was evaluated in a 60-ha, 70-year-old lodgepole pine stand to determine presence or absence of dwarf mistletoe and to identify satellite infection centers that may have originated from vector-carried seed. Of 1,450 plots, 218 were located in a non-lodgepole pine type. Of the remaining 1,232 plots, 871 were infested with dwarf mistletoe. Twenty-five satellite infection centers were found within the lodgepole type that otherwise had no mistletoe, or about 1.7 centers/ha. The number of infected trees in these satellite areas ranged from one to 10 trees (mean 3.5). Most of these areas were positioned along the edges of old logging roads or other forest openings favored by birds. All 25 satellite infection centers were too far removed from main infection centers, or too protected by healthy trees to have originated from seeds expelled from mistletoe fruits alone. Distances from main infection centers ranged from 12 to 65 (ave. 27) m. This portion of the study is continuing and the results will be described in more detail in a subsequent paper.

DISCUSSION

As outlined in this paper, there are several reports of dwarf mistletoe infection centers that originated from other than explosively discharged seeds and that are not remnants of fire escapes. These observations have served as the basis for much speculation that vectors are responsible for disseminating dwarf mistletoe seeds. Dissemination by vectors would explain the origin of satellite infection centers far removed from main infection centers. The vector idea is logical because the sticky seeds are expelled

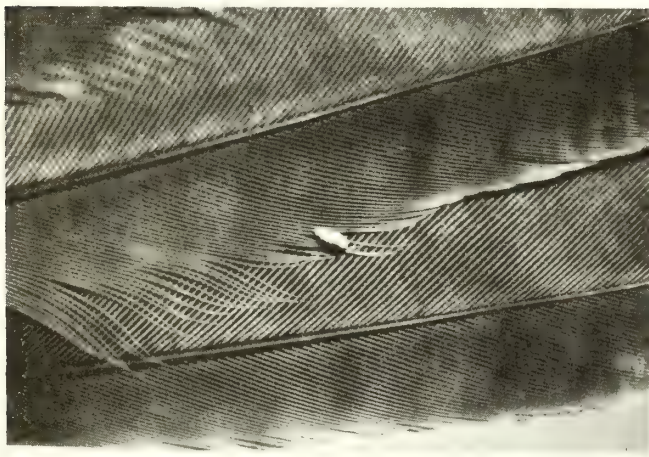


Figure 5.--Dwarf mistletoe seed sticking to the tail feather of a Steller's jay.



Figure 6.--Dwarf mistletoe seed sticking to the tail of a least chipmunk.

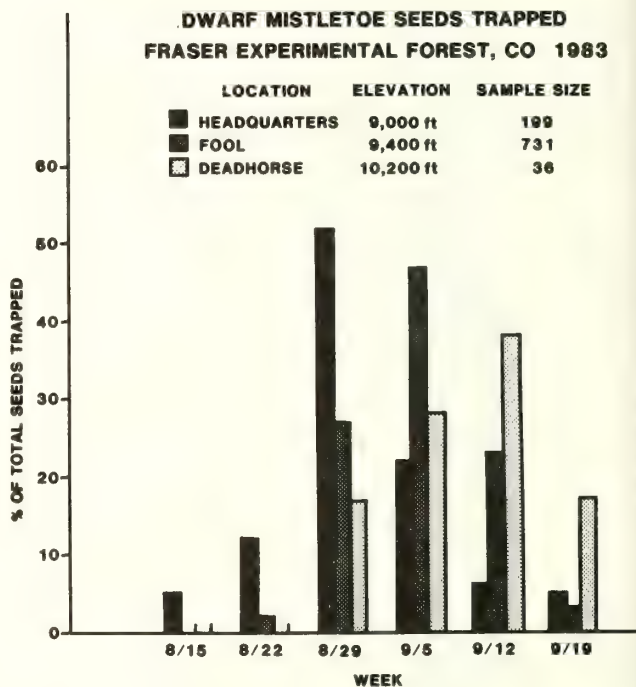


Figure 7.--Number of dwarf mistletoe seeds trapped at three elevations on the Fraser Experimental Forest, Colorado, during 1983.

from fruits at initial velocities of about 27 m per second for distances up to 15 m (Hawksworth and Weins 1972) and will generally stick to anything they hit, including animals. Animals can come in frequent contact with seed when foraging for insects, storing food, and nesting in mistletoe brooms. Further, dwarf mistletoe seeds removed during the animals' regular grooming can cause infection if the seeds are viable and deposited in host trees where infections can occur.

For animals to transport mistletoe seeds that cause infection, certain criteria must be met (Zilka and Tinnin 1976): (1) the seed must become attached to the animal; (2) female seeds must land close enough to a male infection to facilitate pollination and establish seed production because dwarf mistletoe plants are dioecious; (3) the seed must arrive in viable condition on a susceptible host; (4) the seed must come in contact with susceptible parts of the host for infection to occur. Because of these specific requirements, vector-disseminated mistletoe seed infections are probably infrequent, but scattered cumulative infections that develop over a period of time could occur frequently enough to be of concern in the effective control of this parasite.

Our study showed that 22 percent of the birds carried dwarf mistletoe seed during the peak seed dispersal period of A. americanum. Therefore, in a 1,000-bird population, 220 could be carrying seeds at any one time. Several seeds carried by this number of birds could meet all of the above criteria and establish new infections in otherwise healthy stands.

Our study, as well as the other studies reviewed in this paper, has clearly documented that animals can vector dwarf mistletoe seeds and at least two studies showed that birds can inoculate susceptible trees. The movements and behavior of the different vector species play a key role in how and where dwarf mistletoe seed is transported. In general most birds do not eat mistletoe seeds or, if they do, the seeds are not passed through the digestive track in viable condition (Hudler and Hawksworth 1979; Zilka and Tinnin 1976; Ostry et al. 1983). All the reviewed studies show that viable dwarf mistletoe seeds are generally transported on the external surfaces of animals.

The distance seeds can be transported by animals depends upon how large the animals' home range is and whether they are migratory or resident. It is generally believed that mammal vectors are only important in local spread and intensification because of their relatively small home ranges. Resident birds, such as the gray and Steller's jays, mountain chickadees, and gray-headed juncos, are most important in local and short-distance spread of dwarf mistletoe. In our study the gray jay was the most important vector as in the Minnesota studies (Hudler et al. 1974; Ostry et al. 1983).

Migratory birds, such as the warblers (Dendroica spp.), robins (Turdus migratorius), and hermit thrushes (Catharus guttatus), may be more important in long-distance spread of dwarf mistletoes. Many dwarf mistletoe species release seed during the time when some bird species are migrating southward in late summer and fall. Due to habitat specificity, warblers selecting a lodgepole pine habitat in one area will probably choose the same habitat in other areas during migration, if available. During migration, seeds picked up in an infected lodgepole pine stand could be carried and deposited in a lodgepole pine stand some distance away from where the seeds were originally acquired. This habitat specificity is important and increases the chance that a successful infection will result because dwarf mistletoes are generally host specific (Hawksworth and Weins 1972).

CONCLUSION

Several recent studies of vector-dwarf mistletoe relationships have provided definitive documentation that animals do serve as vectors of dwarf mistletoe seeds and that they can inoculate infectable parts of susceptible hosts. Some of the studies show that vectors may be more important in the spread of the parasite than originally thought.

Highly specific requirements must be satisfied before a successful dwarf mistletoe infection can occur. Once infection occurs, several years must pass before the life cycle of this pathogen can be completed to establish an infection center. Although infections resulting from vector-disseminated seed are probably infrequent because of these specific requirements, the cumulative establishment of scattered infection centers over a long period of time and, subsequent local dispersal, can accelerate and intensify the spread of dwarf mistletoes. Once established, each center of dwarf mistletoe infection will remain an inoculum reservoir for future infections unless controlled by silvicultural methods. Knowing where and how to find satellite infection centers that originate from vector-borne seed will enable forest managers to control these areas while they are still small enough to protect commercial stands. Thus, an understanding of the role animals play in the dispersal of dwarf mistletoe seed is essential for the effective control of this damaging forest disease.

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³The effective distance of pollen dispersal in the dwarf mistletoes has not been determined, but pollen dispersal distances for A. americanum of 150 m have been reported in Colorado (Penfield et al. 1976) and dispersal distances of 400 m have been reported in Manitoba (Gilbert and Punter 1984).

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Relationships between Dwarf Mistletoes and Habitat Types in Western Coniferous Forests¹

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Abstract.--Past studies of the relationship between habitat types and the incidence and distribution of dwarf mistletoes are reviewed. Recent productivity studies of several mixed conifer species in relation to habitat type and dwarf mistletoe infection are examined.

INTRODUCTION

During the last decade the use of habitat types to classify forest vegetation (Daubenmire 1952, Daubenmire and Daubenmire 1968) has been expanded to most regions of the western United States (Pfister 1976, Pfister and Arno 1980). A habitat type is usually defined as a unit of land capable of producing similar plant communities at climax (Daubenmire 1968). The habitat type concept is based on the climax stage of succession as defined by Tansley (1935), and reflects an integration of environmental factors that affect forest vegetation. Although a single habitat type may support several seral plant communities, the final stage of plant succession within the habitat type will be a specific climax community. Therefore, habitat type classification systems use climax plant communities as an integrated indicator of environmental conditions that influence plant reproduction, competition, and community development (Steele et al. 1981).

The name of each habitat type is based on the climax community type. The first part of the name is based on the climax tree species and the second part is based on the dominant undergrowth species. Hence the habitat type Pinus ponderosa/Muhlenbergia virescens (Ponderosa pine/screwleaf muhly) is dominated by a ponderosa pine overstory with the ground cover dominated by screwleaf muhly. A series encompasses all habitat types that have the same dominant tree species at climax. Phases of habitat types represent variations in climax plant communities which are less distinct than those between habitat types. Phases may also represent variants of habitat types that are persistent late seral communities (Hanks et al. 1983).

The use of a habitat type classification system does not require the presence of climax vegetation to classify forest land. Habitat types

can usually be recognized during various stages of plant succession by comparing reproduction of tree species present in an area with known successional patterns of a habitat type, and by examination of the dominant undergrowth species present.

Ecological and management implications of habitat types have been expressed in various terms beginning with Daubenmire's 1952 publication. Ecologically, habitat type systems provide a great deal of information concerning the distribution of species for given habitat types, successional patterns and relationships, and the environmental factors influencing these relationships. Resource managers have been developing management implications based on habitat types for timber, range, watershed, and recreation resources (Layser 1974). In addition, application of habitat type systems in research can provide a means of improving the identification of research needs, the design of sampling techniques, and the reporting of results (Layser 1974, Daubenmire 1976).

DWARF MISTLETOES AND HABITAT TYPES

Now let us turn our attention to the relationships between the incidence and distribution of the dwarf mistletoes (Arceuthobium spp.) and vegetation types or habitat types. As early as 1929, Dowding reported that lodgepole pine dwarf mistletoe (Arceuthobium americanum Nutt. ex Engelm.) was more abundant in jack pine (Pinus banksiana Lamb.) stands of the "pine-moss" type than in those of the "pine-heath" type in central Alberta. Her conclusions were based primarily on observations of several jack pine stands representing these vegetation types. The first (and still the most explicit) report of a distinct relationship between the distribution of a dwarf mistletoe and habitat types was made by Daubenmire (1961). He reported that infection by Arceuthobium campylopodum Engelm. on ponderosa pine (Pinus ponderosa Laws.) was common in the Pinus ponderosa/Agropyron spicatum and Pinus ponderosa/Purshia tridentata habitat types. However, infection was not found in five other ponderosa pine habitat types he recognized in eastern Washington and northern Idaho. The habitat types infested with dwarf mistletoe represented the driest and poorest sites for ponderosa pine

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in that region in terms of tree growth and soil texture. Daubenmire and Daubenmire (1968) reported the occurrence of *A. campylopodium* in the *Pinus ponderosa*/*Festuca idahoensis* and *Pinus ponderosa*/*Stipa comata* habitat types in addition to the two habitat types previously cited (Daubenmire 1961). Daubenmire postulated that ponderosa pine was susceptible to dwarf mistletoe only where it was associated with xerophytic grasses and *Purshia*, possibly because the pine grew slowly in these habitat types (Daubenmire and Daubenmire 1968, Daubenmire 1969a, 1969b). Schlatterer (1972) also reported that *A. campylopodium* was most prevalent in habitat types representing low productivity classes for ponderosa pine in central Idaho. In addition, Schlatterer reported a similar relationship between Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) and habitat types he recognized in his Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) series in central Idaho. Dwarf mistletoe incidence and impact was most severe in the habitat type with the poorest productivity potential for Douglas-fir (*Pseudotsuga menziesii*/*Symphoricarpos oreophilus*) and least severe in those habitat types with high productivity (*Pseudotsuga menziesii*/*Calamagrostis rubescens* and *Pseudotsuga menziesii*/Tall Shrubs). In the *Pseudotsuga menziesii*/*Carex geyeri* - *Symphoricarpos oreophilus* habitat type dwarf mistletoe was common on the sites representing poor productivity for Douglas-fir and absent from the high productivity sites. Schlatterer hypothesized that low incidence of Douglas-fir dwarf mistletoe was related to the faster growth rate of Douglas-fir in the highly productive habitat types.

Roe and Amman (1970) collected data on the incidence of *Arceuthobium americanum* in 42 lodgepole pine (*Pinus contorta* Doug. ex Loud.) stands in southeastern Idaho and western Wyoming. Three habitat types were represented in the study: *Abies lasiocarpa*/*Vaccinium scoparium* (ABLA/VASC), *Abies lasiocarpa*/*Pachystima myrsinites* (ABLA/PAMY), and *Pseudotsuga menziesii*/*Calamagrostis rubescens* (PSME/CARU). The relative intensity indexes³ for dwarf mistletoe were 2.5 for the ABLA/VASC habitat type, 1.9 for the ABLA/PAMY habitat type and 1.6 for the PSME/CARU habitat type. Roe and Amman did not speculate on the possible relationships their data may have demonstrated for dwarf mistletoe distribution by habitat types.

Fuller and Hofstetler (1980) reported percent infection and average dwarf mistletoe ratings for lodgepole pine infested by *A. americanum* by understory vegetation (but not habitat types) based on 277 plots located throughout Colorado. These preliminary results indicate relatively large differences for the frequency and severity of dwarf mistletoe between stands dominated by different understory vegetation (Table 1). The data could be stratified by habitat types now that habitat type classifications are available for most of Colorado.

3

Based on a 4 class intensity scale: (1) no infection, (2) less than 1/3 of trees infected, (3) 1/3 to 2/3 of trees infected and (4) more than 2/3 of trees infected.

Table 1.--Lodgepole pine dwarf mistletoe frequency and average mistletoe rating by understory vegetation based on 277 plots from Colorado (from Fuller and Hofstetler 1980).

Predominant Understory Vegetation	% of Plots With Dwarf Mistletoe	Average Mistletoe Rating
<i>Shepherdia canadensis</i>	50	1.3
<i>Vaccinium scoparium</i>	30	1.1
<i>Juniperus communis</i>	35	1.1
<i>Arctostaphylos uva-ursi</i>	23	1.0
<i>Arnica cordifolia</i>	33	1.0
Grasses (no shrubs)	20	0.7

¹ Based on the 6-class dwarf mistletoe rating system, Hawksworth 1977.

The recent findings of Merrill (1983) support the contention that dwarf mistletoes are most prevalent and severe in habitat types that represent xeric or poor sites for their principal host. Her extensive surveys in Colorado demonstrated that the occurrence of *Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens was significantly more frequent in the *Pinus ponderosa*/*Muhlenbergia montana* (PIPO/MUMO) habitat type than in the seven other habitat types sampled (Figure 1). The PIPO/MUMO habitat type represents one of the most xeric habitat types of the ponderosa pine series in Colorado (Hess 1981). In addition, the severity of dwarf mistletoe infection, as indicated by mean dwarf mistletoe ratings based on the 6-class system (Hawksworth 1977), was highest in the PIPO/MUMO habitat type. The mean dwarf mistletoe rating of this habitat type was significantly higher than five of the habitat types, but not significantly higher than two of the habitat types she sampled.

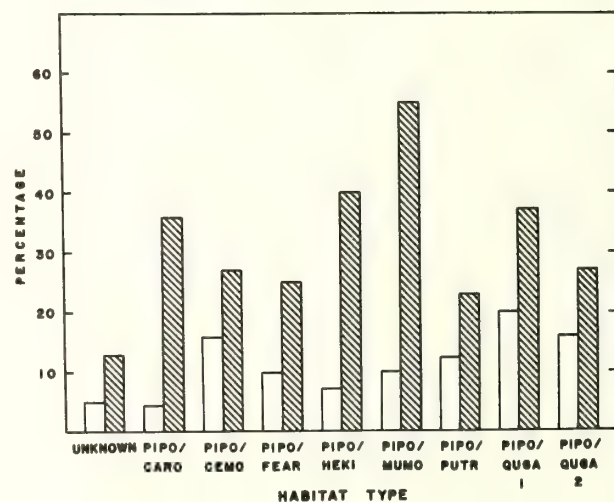


Figure 1.--Relationship between incidence of ponderosa pine dwarf mistletoe and habitat type on 547 plots in Colorado. The open bars show the percent distribution of plots by habitat types and the cross-hatched bars show the percent of plots with dwarf mistletoe in each habitat type (from Merrill 1983).

Hawksworth (1959, 1961, 1969, 1975) has considered many of the ecological factors that could influence the distribution of dwarf mistletoes. These factors include stand history, temperature, site quality, elevation, topography, and aspect. There appear to be fairly well defined relationships between some dwarf mistletoes, the elevational ranges of their principal hosts, and topographic features such as slope steepness, slope position, and aspect (Hawksworth 1969). Merrill (1983) examined these factors in relation to those habitat types with the highest incidence and severity of *A. vaginatum* subsp. *cryptopodum*. She found a high degree of correlation between habitat types, topographic features, and elevational positions and high incidence of dwarf mistletoe.

Much of the information available concerning the relationships between dwarf mistletoes and habitat types is found in the many habitat type classifications completed in the western United States. Several classifications have provided only qualitative data, reporting distribution and incidence of dwarf mistletoes by habitat types as low, minor, present, uncommon, moderate, high, damaging, severe, prevalent, or significant (Hall 1973, Voland 1982, Henderson et al. 1977, Hopkins 1979a, 1979b, Hanks et al. 1983). For example, Hanks et al. (1983) presented the percentage of stands sampled with light to heavy infection by *A. vaginatum* subsp. *cryptopodum* for a single ponderosa pine habitat type in northern Arizona. Incidence of mistletoe in their remaining ponderosa pine habitat types were reported as a qualitative rating from light to heavy (Table 2). Another classification has rated habitat types as either highly susceptible or resistant to mistletoe infection (Schlatterer 1972), but this use of terminology is misleading.

Only a few habitat type classifications have attempted to provide quantitative data on the incidence of dwarf mistletoes for different habitat types. Daubenmire and Daubenmire (1968) listed the number of stands they sampled where *A. campylopodum* was present for each habitat type in their ponderosa pine series. Franklin and Dyrness (1973) provided constancy and coverage figures for *A. campylopodum* in habitat types based on Daubenmire and Daubenmire's (1968) data. Pfister et al. (1972) reported percentages of plots sampled by habitat type that had Douglas-fir or larch mistletoe (*Arceuthobium douglasii* or *A. laricis* (Piper) St. John) present in light, moderate, or severe levels (Table 3). However, they did not include this information in their final habitat type classification for western Montana (Pfister et al. 1977).

If it appears we have little information regarding the distribution of dwarf mistletoes by habitat types, we have even less information on the growth loss and mortality caused by these parasites in different habitat types. Moir and Ludwig (1979) reported that *A. abietinum* Engelm. ex Munz reduces height growth of white fir (*Abies concolor* (Gord. & Glend.) Lindl.) in the *Abies concolor*-*Pseudotsuga menziesii*/Sparse Understory habitat type on the Kaibab Plateau. However they did not provide quantitative data to support their contention. Ziegler (1978) reported significant

Table 2. Incidence of *Arceuthobium vaginatum* subsp. *cryptopodum* by ponderosa pine habitat types in northern Arizona (from Hanks et al. 1983).

Habitat Type ¹	Incidence of Dwarf Mistletoe
PIPO/MUVI; Typical Phase	Damage light to moderate in 77% of stands
PIPO/MUVI; QUGA Phase	Light to moderate mistletoe in 70% of stands
PIPO/MUVI-FEAR; Typical Phase	Light, moderate, heavy levels in equal frequencies
PIPO/MUVI-FEAR; QUGA Phase	Light to moderate mistletoe
PIPO/FEAR; Typical Phase	Present in moderate to heavy amounts
PIPO/FEAR; QUGA Phase	Moderate to heavy mistletoe
PIPO/FEAR; BOGR Phase	Moderate to heavy mistletoe
PIPO/BOGR; Typical Phase	Light to moderate mistletoe
PIPO/BOGR; PIED Phase	No mistletoe data given
PIPO/BOGR; QUGA Phase	Mistletoe incidence light
PIPO/BOGR; ARTR Phase	Light to heavy mistletoe

¹See Hanks et al. (1983) for meaning of habitat type abbreviations.

toe-infected lodgepole pines in some habitat types, but not in others, in the vicinity of Crater Lake, Oregon. He also demonstrated a significant reduction in five-year basal area increment with increasing levels of mistletoe infection in the *Pinus contorta*/*Carex-Lupinus* community. However, heavy mistletoe infection did not affect sapwood thickness in lodgepole pine in any of the habitat types sampled.

RELATIONSHIPS OF DOUGLAS-FIR DWARF MISTLETOE WITH HABITAT TYPES IN THE SOUTHWEST

We compared ten-year periodic annual increment for dominant and codominant Douglas-firs between nine southwestern habitat types (Mathiasen and Blake 1984). Data were collected from spruce-fir and mixed conifer stands in Arizona and New Mexico from 1979 to 1981. Diameter at breast height (DBH, nearest 0.1 inch), DMR (six-class system, Hawksworth 1977), crown class (dominant, codominant, intermediate, suppressed), and five- and ten-year radial growth at DBH were recorded for a total of 27,000 Douglas-fir trees.

Ten year periodic annual increment (PAI) for dominant, codominant, and intermediate Douglas-firs was significantly different at $p = 0.10$ in all the habitat types studied regardless of DMR class. Heavy Douglas-fir dwarf mistletoe infec-

Table 3.--Observance of Douglas-fir (DF) and larch (WL) dwarf mistletoe for twelve habitat types in western Montana (from Pfister et al. 1972).

Habitat Type ¹	Stands Sampled N	Stands w/DF n	Douglas-fir				Stands w/WL n	Western Larch			
			None	Light	Moderate	Severe		None	Light	Moderate	Severe
			Percent					Percent			
PSME/CARU	15	15	60	13	13	13	2	0	0	0	0
PSME/ARUV	10	10	60	20	10	10	3	0	0	0	0
PSME/VACA	15	15	80	20	0	0	14	64	14	7	14
PSME/SYAL	23	23	52	22	22	4	5	75	0	25	0
PSME/PHMA	25	25	56	24	8	12	7	86	0	14	0
PSME/XETE	15	15	53	27	7	7	7	100	0	0	0
ABGR/CLUN	10	10	80	10	10	0	7	86	0	0	14
ABLA/CLUN	17	15	60	7	27	7	11	27	0	27	45
ABLA/XETE-CARU	9	8	88	0	0	12	5	100	0	0	0
ABLA/CLUN-VACA	7	6	100	0	0	0	5	100	0	0	0
THPL/CLUN	8	8	63	12	12	12	8	25	25	25	25
TSHE/CLUN	7	5	100	0	0	0	6	17	17	50	17

¹See Pfister et al. (1977) for meaning of habitat type abbreviations.

tion significantly reduced ten-year PAI in all the habitats. Moderate infection significantly reduced growth in the *Picea pungens*-*Picea engelmannii*/*Erigeron superbis* and *Abies concolor*-*Pseudotsuga menziesii*/Sparse Understory; *Robinia neomexicana* Phase habitat types. In addition, the percentages of growth reduction (cubic feet/acre/year) for moderate and heavily infected Douglas-firs varied greatly between habitat types (Table 4). A potential damage rating representing damage due to dwarf mistletoe was assigned to each habitat type by adding percent growth reduction for moderately (DMR class 3-4) and heavily (DMR class 5-6) infected trees.

Table 4. Percent growth reduction for dominant and codominant Douglas-firs by DMR classes 3-4 and 5-6 and potential damage ratings by habitat in Arizona and New Mexico (from Mathiasen and Blake 1984).

Habitat Type ¹	% Growth Reduction		Potential Damage Rating
	DMR 3-4	DMR 5-6	
PIPU-PIEN/ERSU	31	63	94
ABCO-PSME/ACGL; BERE Ph.	20	65	85
ABCO-PSME; RONE Ph.	25	59	84
ABCO-PSME; BERE Ph.	0	75	75
ABCO-PSME/ERSU	8	65	73
PIPU-PSME; VAAC Ph.	10	55	65
ABCO-PSME/POFE	15	48	63
ABCO-PSME/ ACGL; HODU Ph.	0	60	60
ABLA/ERSU	4	53	57
PIPU-PIEN/SECA	0	45	45
ABLA/VASC-LIBO	0	44	44
ABCO-PSME/QUGA	0	24	24

¹See Moir and Ludwig 1979 for meaning of habitat type abbreviations.

CONCLUSIONS

In summary, we can conclude that we know little about the relationship between habitat types and dwarf mistletoe distribution and severity at present. The only pattern that appears to be developing thus far is the relationship of high incidence and severity of dwarf mistletoe infection for two (and possibly three) *Arceuthobium* spp. in habitat types that represent low productivity or xeric sites for their principal hosts (Daubenmire 1961, 1969a, 1969b, Daubenmire and Daubenmire 1968, Schlatterer 1972, Merrill 1983). The majority of information on the incidence and severity of dwarf mistletoe infection by habitat types is primarily qualitative and based on relatively small sample sizes. In addition, only Merrill's (1983) and Fuller and Hofstetler's (1980) reports have been based on random sampling designs. We need to conduct additional studies utilizing random sampling techniques with larger sample sizes taken over a wide geographic range to better understand the relationships between dwarf mistletoes and habitat as stand and fire history, climate, elevation, and topography and dwarf mistletoe habitat types and dwarf mistletoe (Hawksworth 1969, Alexander and Hawksworth 1976, Wicker and Leaphart 1976).

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The Effect of Dwarf Mistletoe on Forest Community Ecology¹

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Abstract.--Dwarf mistletoes cause significant changes in the structure and function of individual host trees. For example, the effects on lodgepole pine include modified rates of physiological process (e.g., decreased rates of respiration for infected trees), different structural characteristics of twigs and needles (e.g., reduced needle and twig mass), and different branch growth patterns associated with witches' broom formation. These effects on individual trees imply several related changes in the communities of which the trees are a part. Indeed, in the stands selected for study, where lodgepole pine was the dominant species, the changes in the individual trees, due to infection by dwarf mistletoe, contribute to visual differences in the structure of the entire community. These structural differences imply functional differences. Quantification of both, and correlation with the level of infection by dwarf mistletoe, is now in progress. This interplay between parasites and community dominants suggests a convenient tool to examine the ecological effects of stress and chronic disturbance on community dynamics.

INTRODUCTION

Host-parasite associations are both intimate and complex. They are the result of intricate interrelationships between two species, one of which (the host) provides part or essentially all of the environment for the other (the parasite). Simultaneously the parasite causes changes in its host. The degree of change in the host ranges from slight to extensive, but as it increases, the relationship between the host and its environment also changes. The overall effect is that parasitism can set in motion a chain of events which may have profound effects on communities in which the parasites are active (Holmes 1979).

Parasites are a part of all communities and thereby influence the structure and function of all communities (Price 1980). While this point is known and appreciated, the effect of parasitic plants on plant communities remains to be more completely elucidated. A group of parasites which is superbly suited to the study of parasitic

impact on the dynamics of plant communities are the dwarf mistletoes (*Arceuthobium* spp.). In western North America, dwarf mistletoes are common, easy to find, relatively easy to sample, they have slight to severe effects on their host, and their hosts dominate communities which develop under a wide selection of ecological conditions (Hawksworth and Wiens 1972, Parmeter 1978). That dwarf mistletoes change the structure and function of their host, and thereby of any community of which they are a part, is obvious. The characteristic growth response of most host species, called witches' brooms, illustrates the point (fig. 1). This is but one of the several changes which take place following infection. The point is: what are the quantitative differences between communities with and without dwarf mistletoe?

Parmeter (1978) provided an excellent summary of the dynamics of communities infected with dwarf mistletoe. He noted that these parasites cause a reduction in the growth, wood quality and longevity of their host. The extent of the reduction is dependent on such factors as the number of infections in the tree crown, their position in the crown, the rate of infrapopulation increase, and the extent of witches' broom formation. The extent to which any of these factors affect the host trees depends on many variables (e.g., site quality, host vigor, host resistance, host crown characteristics, stand density, stand age, stand structure and stand

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history). While the multiplicity of interacting factors and variables will make determination of the quantitative effects of parasites on their host community difficult, the answer can nevertheless be obtained.

If an uninfected stand is invaded by dwarf mistletoe, there are several changes in stand structure that can be predicted. One change, having significant economic consequence, is an eventual reduction in stand volume (see Scharpf and Parmeter 1978). Although the effect of infection on tree growth is quite variable, the reduction in stand volume is associated with such things as reduction in bole diameter, height, and/or changes in taper (Baranyay and Safranyik 1970, Hawksworth and Hinds 1964), poor wood quality, mortality, and secondary loss due to insect damage, decay and the increased effect of

certain abiotic factors (Hawksworth and Wiens 1972). Reductions in the root system of the host have also been reported (Knutson and Toevs 1972). These reductions in growth not only affect individual tree size and thereby stand productivity, but they also affect such ecological processes as competitive interaction. Harper (1977) reports various cases of increased densities of smaller plants in relatively infertile soil and lower densities of larger plants in fertile soil. He suggests that fertile soils, which contribute to increased rates of plant growth, increase "population pressure" leading to fewer plants of greater stature. If dwarf mistletoes decrease host growth, thereby reducing the intensity of competition, heavily infected stands could be expected to be composed of a greater number of smaller trees as compared with uninfected stands.

When an increase in mortality follows infection (Hawksworth and Wiens 1972), one would predict a somewhat greater turnover rate for individuals within the stand. This change would influence host population dynamics which in turn would affect the relative stability of stand composition and/or the rates of stand development in association with successional trends. The potential of increased frequency and intensity of fire in infected stands also contributes to increased mortality (Alexander and Hawksworth 1975, Wicker and Leaphart 1976). Stand conditions, which would otherwise support relatively cool, surface fires, can be changed to conditions which support much more intense fires due to fuel accumulation through the death or senescence of broomed branches or trees. These fires can, of course, rapidly change stand structure and exclude dwarf mistletoe locally. However, these fires can also produce suitable conditions for the reestablishment of young, vigorous, seral stands composed of some host species which otherwise would tend to be eliminated from climax stands. Where dwarf mistletoe attacks these seral species, mistletoes and fire can interact synergistically to maintain stand conditions well suited to the perpetuation of dwarf mistletoe infection.

Changes in the structure of individual trees also leads to the development of unique habitats for some animal species (Tinnin et al. 1982). Animals, or their nests, frequently are found in association with dense brooms.

All of the structural changes noted above are associated with functional changes as well. Among the functional changes which occur are an increase in water loss from the host due to transpirational losses from the aerial shoots of the dwarf mistletoe (Fisher 1975), selective localization of certain minerals in and/or near sites of infection by dwarf mistletoe (McDowell 1963), changes in rates of respiration and photosynthesis (Clark and Bonga 1970), and changes in the occurrence and concentration of growth regulators (Paquet 1979, Schaffer et al. 1983). The significance of these



Figure 1.--Lodgepole pine infected with lodgepole pine dwarf mistletoe. Notice the large brooms at the base of the crown.

functional changes has not been completely determined but the fact that they exist points to the reality of significant modification of host metabolism.

STUDIES IN PROGRESS

This section summarizes work in progress or work not yet published. Several studies of communities of lodgepole pine (*Pinus contorta*), uninfected and infected with lodgepole pine dwarf mistletoe (*A. americanum*), have been initiated. The communities studied are located on the east flank of the Cascade Mountains in Oregon. These pine forests are ecologically less complex than other forest types so are ideal for a preliminary study of effects of dwarf mistletoe on the dynamics of forest communities. Two different sites have served as the focus of study. Stand density at the sites was 0.3 trees/m² at site 1 and 0.2 trees/m² at site 2 for the overstory, and 1.2 trees/m² and 1.8 trees/m² respectively for all lodgepole pine present, regardless of size (Larsen 1981). The mature trees averaged 84 and 88 years old, 25 cm and 26 cm in diameter at breast height and had an average height of 13 m and 14 m respectively for the two sites.

In order to understand the effects of dwarf mistletoe on biomass reallocations within trees, I have begun to examine the difference in growth form between lightly infected and heavily infected trees. Adjacent small trees (<5.2 m tall) were felled a pair at a time and removed to the laboratory. They were dismantled branch by branch and the dry mass (48 hours at 80 C) of the needles and twigs of each was measured. The mean annual mass increment of the heavily infected trees was 87% of the lightly infected trees. Preliminary samples have shown that with severe infection, relatively more mass is found in branch wood than in trunk wood, and the mass of needles to wood tends to be less on heavily infected trees (table 1). The changes in mass are due primarily to the large brooms that form in the lower crown (fig. 1).

Broshot (1982) looked at specific characteristics of needles and twigs and found additional structural differences between healthy and infected trees (table 2). She found a significant decrease in needle number, needle length, needle biomass, twig length and twig mass per annual grown segment for individual twigs from branches which supported dwarf mistletoe. Based on these data and using the procedures of Mellor and Tregunna (1972), she also found a significant decrease in needle surface area.

I am studying the number of needles and twigs in infected and uninfected branches of approximately equal age. The results to date show much higher populations of needles and twigs on systemically infected branches (witches' brooms). The higher population of needles is due to the higher population of twigs rather than more needles per twig. As the number of needles and twigs increases, correspondingly there is an increase in the mass of branch wood and branch needles. However, wood mass tends to increase at a greater rate than photosynthetic tissue (the number of needles). This trend is associated with needles of lesser individual mass (Broshot 1982). Thus, systemic brooms are composed of a greater number and total mass of smaller needles on a more massive and profusely branched limb. These results are similar to those reported for Douglas-fir (Tinnin and Knutson 1980). The implications of these findings are that physiological phenomena, such as moisture loss and CO₂ exchange, are affected.

The data reported above show substantial reallocation of host biomass following infection. These structural changes are associated with several functional changes. Broshot (1982) showed that needles from infected branches contained 2 to 3 times more starch than uninfected needles. The twigs showed a similar but less pronounced response. Similar results are reported for the hosts of other plant parasites as well (Allen 1942, Inman 1962, MacDonald and Strobel 1970, Daly 1976). There are several possible explanations for Broshot's observation. One which is

Table 1.--Relative mass of the aerial portions of lodgepole pine infected by lodgepole pine dwarf mistletoe (sample is too small for valid statistical analysis).

	Mass as Percent of Total		Ratio
	Light ¹ Infection	Heavy ² Infection	(Heavy/Light) ³
Needles	21	17	.82
Limbs	17	28	1.69
Trunk	62	55	.87
Sample size	4	4	--

¹No large brooms present and relatively few local infections.

²At least one relatively large broom and numerous local infections.

³Ratios are based on original mass data, not the percentages reported in this table.

Table 2.--Changes in needle characteristics of lodgepole pine as a result of infection by lodgepole pine dwarf mistletoe (from Broshot 1982).

Mean Needle Characteristics	Site	Branch Infection Type ¹		
		None	Local	Systemic
Number/annual segment	1	85 a	53 b	47 c
	2	58 a	42 b	--
Length (cm)	1	4.1 a	3.4 a	2.1 b
	2	3.5 a	2.9 b	--
Mass/annual segment (g)	1	1.59 a	.68 b	.32 c
	2	.73 a	.39 b	--
Surface Area/annual segment (cm)	1	795.6 a	671.4 b	409.1 b
	2	693.8 a	575.5 b	--
Sample Size	1	4	41	20
	2	13	21	0

¹Differences shown are significant at the 5% level of confidence.

particularly interesting to me is the possibility that the whole infected branch is a carbon sink on the host tree (Clark and Bonga 1970). Leonard and Hull (1965) reported only limited movement of photosynthate into intact infected branches but they were examining relatively small branches. The sink hypothesis requires further testing.

A related study by Wanner and me (unpublished data) has shown that the metabolic rates of the host are also affected. We found that the rate of photosynthesis of infected trees tends to be somewhat higher than that of uninfected trees. This is consistent with what Clark and Bonga (1970) reported for spruce. However, we found the rate of respiration of infected trees to be significantly lower than that of uninfected trees (table 3). This is not consistent with what Clark and Bonga reported. We also found that the dwarf mistletoe respired significantly faster than either healthy or infected tree tissues, an

observation consistent with McDowell (1963) and Fisher (1975). (There are no data available on the rate of respiration of root tissue in infected trees.) While it is tempting to assume that higher rates of photosynthesis and lower rates of respiration explain the increased levels of starch in the infected host tissues of lodgepole pine, such an assumption is premature until more is known about infected branches as resource sinks.

Dwarf mistletoes are known to affect the reproductive potential of their host. Schaffer et al. (1983) found reductions in cone and seed size on infected trees. Wanner (personal communication) has found significant reductions in cone number as well. He also found a significant decrease in the number of germlings in infected stands although there are noticeably more seedlings and saplings in infected stands. The importance of these changes is now being investigated.

Table 3.--Rates of dark respiration for different tissue samples from lodgepole pine and lodgepole pine dwarf mistletoe.

Tissue Type	n	Rate ¹	p<.05
Needles from uninfected tree	22	286	a
Needles from uninfected branch from infected tree	22	218	b
Needles from infected branch	22	200	b
Aerial shoots	22	438	c

¹ $\mu\text{l O}_2 / \text{g} \cdot \text{hr}$, standardized to 20°C.

EFFECTS OF PARASITISM ON COMMUNITIES

The changes in structure and function of host trees noted above provide ample qualitative evidence of changes in the structure and function of the forest community. A great deal is known about infra- and suprapopulations of dwarf mistletoe, and of the effects of dwarf mistletoe on the host population. With regard to fire ecology, there is some information on community dynamics, but with an orientation towards timber management (see Zimmerman and Lavern, these proceedings). What is markedly absent is information on the general ecological effects of dwarf mistletoe on the basic structure and function of the host community as a whole. One is left to ask: what are the changes in community structure and function which occur subsequent to the introduction of dwarf mistletoe?

If one were to characterize important structural features of a forest community, these would include changes in stand density, species composition and diversity, physiognomy and spatial patterns of dispersal. Do dwarf mistletoes affect any of these characteristics? The answer is, of course, yes. As already discussed, changes in mortality, fire frequency and susceptibility to infection all directly affect forest community structure. Similarly, one might characterize productivity and mineral cycling as important functional attributes of a forest community. Again, little is known of the effect of dwarf mistletoe on these processes.

What is known or suspected at the present time is that dwarf mistletoes may contribute to higher stand density, less mass per individual tree, lower canopy height, lower germling densities due to lower seed density per unit area, better seedling survival with higher total seedling density, higher plant and animal species diversity, and greater variation in tree growth form. The effects on such community processes as productivity and nutrient cycling are not apparent to me and clearly need study. These are but a few of the actual changes which eventually will be described. These few points are nonetheless significant as a reminder of how important parasites are in natural ecosystems. Parasites collectively do much to shape plant communities but many of the effects have yet to be evaluated in detail. Dwarf mistletoes are but one genus among the many parasitic genera present and even so have a dramatic effect on the communities of which they are a part. A major reason the effect is so marked is that dwarf mistletoes frequently attack community dominants. Any resulting change in the dominants will be expressed throughout the rest of the community.

In summary, there are many ecological differences between infected and uninfected stands. They exist as differences in both structure and function. No evaluation of communities, without attention to the subtle variable of parasitism, can lead to proper interpretation of community process. The possible applications of such studies would be toward a

better understanding of the effects of mild chronic disturbance and slight increases in stress on forest community structure and function. As such, the potential for study is tremendous and the importance of elucidating these significant forest dynamics would be difficult to overemphasize.

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Ecological Interrelationships of Dwarf Mistletoe and Fire in Lodgepole Pine Forests¹

G. Thomas Zimmerman and Richard D. Laven²

Abstract.--Dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) is the most serious disease agent in lodgepole pine (*Pinus contorta* Dougl.) forests. Fire represents the ecological factor most responsible for the structure and distribution of lodgepole pine forests and the frequency and intensity of dwarf mistletoe infection. In southwestern Colorado lodgepole pine stands, dwarf mistletoe infection intensity and frequency are most closely related to the frequency of fires per year. As the number of fires per year increase, average stand dwarf mistletoe ratings decrease. Other fire history attributes such as the number of years since the last fire and the average length of time, in years, between fires do not appear to strongly influence dwarf mistletoe spread and intensification. Fire exclusion in these forests has not facilitated increased infection by dwarf mistletoe. However, a continuation of this policy, in the absence of alternative mechanisms of regulation, will allow rapid and progressive dwarf mistletoe spread and proliferation.

INTRODUCTION

Lodgepole pine is a coniferous forest species which is extremely abundant and widespread throughout the western United States and Canada. The ability of this species to establish and develop under a broad range of environmental conditions and throughout a wide geographic range is greater than nearly every other coniferous species found in North America (Pfister and Daubenmire 1975). This substantially wide ecologic amplitude, in combination with reproductive adaptations that favor establishment and growth following fire, contribute to the wide distribution and importance of these forests.

Fire functions as a dominant force in the development of lodgepole pine forests and may be the single most important factor influencing stand establishment and structure (Wellner 1970, Brown 1975). The variation in intensity occurring during a fire, amount of stored seed available, and the probability of a seedling becoming established influence the post-fire physical development of lodgepole pine stands (Lotan and Jensen 1970, Brown 1975). Differential intensity levels occurring during past fires is responsible for present day stand structure

in the central Rocky Mountains. Extensive even-aged stands are attributable to high intensity fires while the presence of uneven-aged stands confirm the occurrence of low intensity fires (Leiberg 1904, Smithers 1961).

Although fire represents an important and complex force, dwarf mistletoe also constitutes an important ecological factor in lodgepole pine forests. This disease, present in nearly 50 percent of all stands in Colorado, has marked effects on forest growth and structure.

Lodgepole pine dwarf mistletoe is an obligate parasitic seed plant having no fire-enduring or fire-evading mechanisms (Rowe 1983). Its survival then, is contingent upon fire avoidance. But, since the host attacked by this pathogen is fire-dependent, fire-avoidance is difficult.

Fire, therefore, represents an ecological factor capable of either directly or indirectly influencing dwarf mistletoe growth and proliferation. Direct effects result in mortality from tissue oxidation and reduction of the parasite plants to ash, or from destruction of the host tree (Wicker and Leaphart 1976). Indirect effects, such as smoke or temperature influences, may influence parasite reproduction and limit further infection. Such indirect effects can impact the parasite plants much more severely than host trees (Koonce and Roth 1980).

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Wildfire is frequently suggested to be the major factor influencing dwarf mistletoe in lodgepole pine forests (Dowding 1929; Gill and Hawksworth 1961;

Taylor 1969; Baranyay 1970; Heinselman 1970, 1973, 1978; Kiil 1974; Fellin 1980). However, few, if any, studies have quantitatively established the role of fire occurrence in regulating dwarf mistletoe populations (Hawsworth 1961, 1975; Wright and Heinselman 1963). In addition, the effects of fire absence on dwarf mistletoe spread and intensification are not well understood (Brown 1975).

This study was undertaken in an attempt to improve our understanding of the reciprocal relations between dwarf mistletoe and fire in lodgepole pine forests. Specific objectives were:

1. To investigate the relationship between dwarf mistletoe frequency and abundance and wildfire history; and
2. To assess the effects of fire suppression on dwarf mistletoe spread and intensification.

STUDY AREA

Areas of the Gunnison National Forest in Gunnison County, Colorado served as the study location. Specific study sites were located in the Taylor Park area of the Taylor River Ranger District in southwestern Colorado. Taylor Park, located approximately 61 km northeast of Gunnison, is a high elevation mountain valley bounded on the north and east by the continental divide. Study site elevations range from 2920 to 3200 m and slopes vary from nearly flat to moderately sloping. Fifteen separate sites located throughout Taylor Park were chosen for sampling. Stands were selected on the basis of: the absence of any forest development activity (ie thinning, harvesting, etc.), presence of fire-scarred trees, differences in age classes, and dispersal throughout the study area. Rectangular plots ranging from 150 to 375 m² were established in each stand for tree measurements.

METHODS

Measurements were taken at each site to provide information regarding dwarf mistletoe infection intensity, time since infection, stand age, and fire history. Dwarf mistletoe infection intensity was evaluated by determining a dwarf mistletoe rating for each tree tallied in each plot and then computing an average stand dwarf mistletoe rating (DMR). Dwarf mistletoe ratings for each tree were determined by using the 6-class rating system (Hawsworth 1977). Average stand rating (DMR) was calculated by totaling individual tree ratings and dividing by the total number of trees.

Time since infection by dwarf mistletoe (TSI) was determined by a method similar to one described by Scharpf and Parmeter (1966). Cross sections were removed from infected stems and examined with a microscope to facilitate a count of the annual growth rings from the bark to the ring nearest the innermost portion of the longest parasite sinker. Stem infections suitable for determining time since infection were only found in three plots. In the remaining plots, time since infection was estimated

indirectly from average stand dwarf mistletoe rating. Using data presented by Hawsworth and Hinds (1964), the following relationships between DMR and time since infection were developed:

If average stand DMR greater than 0 but less than .6, then time since infection = average stand DMR/.06

If DMR greater than .6 but less than 2.2, then time since infection = ((average stand DMR - 2.2)/.08) + 10

If DMR greater than 2.2 but less than 4.0, then time since infection = ((average stand DMR - 2.2)/.09) + 30

If DMR greater than 4.0 but less than 4.6, then time since infection = ((average stand DMR - 4.0)/.06) + 50

If DMR greater than 4.6, then time since infection = ((average stand DMR - 4.6)/.03) + 60

Tree age was assessed by collecting two increment cores at ground level from a random sample of 25 percent of all live trees. Age was estimated by examining the cores under a microscope and counting annual rings.

Fire history was determined from dating of fire scar samples from live trees. Complete cross sections were removed from at least two fire-scarred trees at each sampling site. Dates of fires were determined for each of these trees by counting, with the aid of a microscope, the number of annual rings from the sampling year (1983) to the most recent scar and between previous scars.

For each sampling area the mean fire return interval was calculated by deriving the arithmetic average of the number of years between each two successive fires, except when only one fire event was documented. In this instance, the fire return interval was taken as the time from that fire to the present and will continue to increase until the next fire occurs. Time since the last fire was estimated by determining the number of years from the sampling year to the most recent fire event. Fire frequency was computed by dividing the number of fires recorded for each site by the age in years of the oldest living fire-scarred tree sampled in 1983.

Stage II inventory data on file at the Taylor River Ranger District were also reviewed to gain additional dwarf mistletoe rating and stand age information. Average stand age and DMR data from 122 additional lodgepole pine stands were reviewed and used for comparison with age and DMR data collected during this study.

RESULTS AND DISCUSSION

Dwarf Mistletoe Infection Intensity

Dwarf mistletoe infection was present, to some degree, in 100 percent of the stands sampled in this study. When compared by individual DMR class inter-

vals, the greatest percentage of stand were infected at the highest level (DMR = 5.1-6.0), followed by the immediately lower two class intervals (DMR = 4.1-5.0 and 3.1-4.0). Distribution of lodgepole pine stands by DMR class intervals in Taylor Park was:

DMR class interval	Percentage of stands infected
0	0
0.1 - 1.0	13.3
1.1 - 2.0	6.7
2.1 - 3.0	6.7
3.1 - 4.0	20.0
4.1 - 5.0	20.0
5.1 - 6.0	33.3

Over 70 percent of these lodgepole pine stands contained dwarf mistletoe infections with intensities greater than 3.1.

Time Since Infection

Because the time since infection was computed on the basis of the average stand dwarf mistletoe rating, it closely followed the trend observed in infection intensity levels. Specifically, as DMR increased so did the time since infection. Consequently, over 70 percent of all sampled stands had been infected for 40 years or longer.

For those stands where stem infections were used to age infections, time since infection was also computed by the same method as for other stands. For all three stands, the age of the stem infection was very close to the estimated time since infection. In one stand, the two methods produced an identical time since infection.

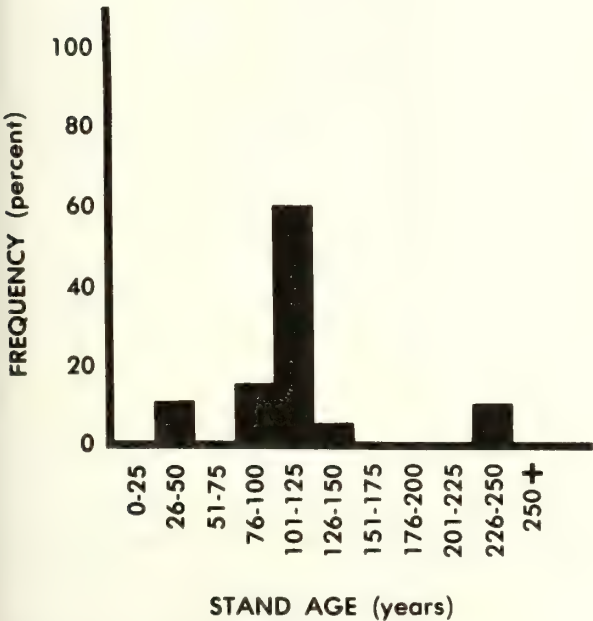


Figure 1.--Frequency histogram of lodgepole pine stand age in Taylor Park, Colorado.

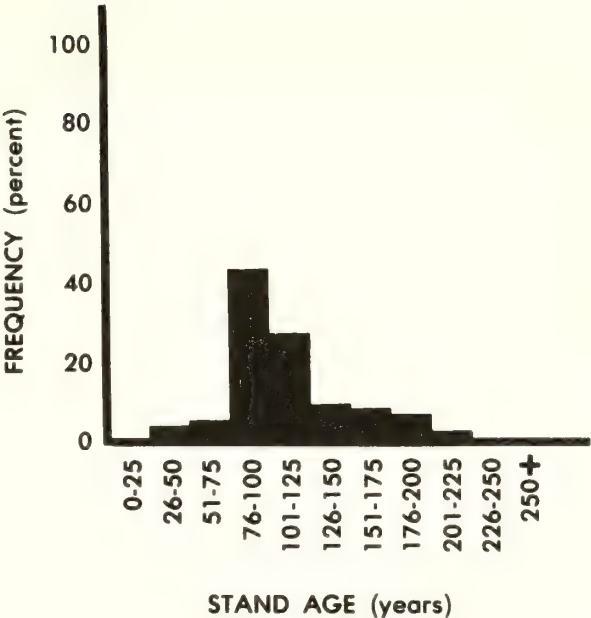


Figure 2.--Frequency histogram of lodgepole pine stand age in Taylor Park, Colorado (source = USFS inventory data).

Stand Age

Analysis of age class distribution of lodgepole pine stands in the Taylor Park area revealed that stands were most frequently between 101 and 125 years old (fig. 1). Sixty percent of all measured stands occurred within this age range. Stands representing young and mature age classes were noticeably lacking (fig. 1).

Analysis of the age class distribution of the additional stands surveyed in the Stage II forest inventory revealed similar trends. The greatest percentage of stands were found in age classes of 76-100 and 101-125 years (fig. 2). These age ranges consisted of 43 and 26 percent of all stands respectively. Again, young age stands were lacking; only eight percent of all stands were between 1 and 75 years in age. Frequency of stands older than 125 years showed a continual decline with increasing age (fig. 2).

Fire History

The most active period of fire occurrence in the Taylor Park area as indicated from fire scar analyses was between 1858 and 1882 (101 to 125 years before the measurement year, 1983) (fig. 3). Numbers of fires occurring before the peak were much lower. A decline in fire occurrence, as indicated by scarred trees, occurred during the last 100 years.

Considerable variation between the sampled stands was observed in the time since the last fire, mean fire return interval, number of fires during the life of the stand, and fire frequency (table 1). Time since the last fire varied from as low as seven to as high as 132 years. Observed mean fire return intervals were as low as four years and as high as

Table 1.--Fire history characteristics and stand age of sampled stands in Taylor Park, Colorado.

Stand #	Ave. Age (years)	Time since last fire (years)	Mean fire return interval (years)	Number of fires	Fire frequency (fires/year)
09	111	47	41	3	.013
11	47	7	17	7	.056
12	122	102	10	6	.023
13	33	51	10	4	.047
14	115	104	4	4	.032
17	107	22	25	5	.022
18	109	50	38	3	.013
19	93	103	27	4	.017
38	124	24	31	8	.029
139	114	132	133+ ¹	1	.003
239	227	132	133+ ¹	1	.003
140	122	121	70	3	.010
240	236	121	70	3	.010
141	83	92	8	6	.028
241	103	92	8	6	.028

¹This stand has only one fire record, thus, the fire return interval has been taken as the time from that fire to the present and will continue to increase until the next fire occurs.

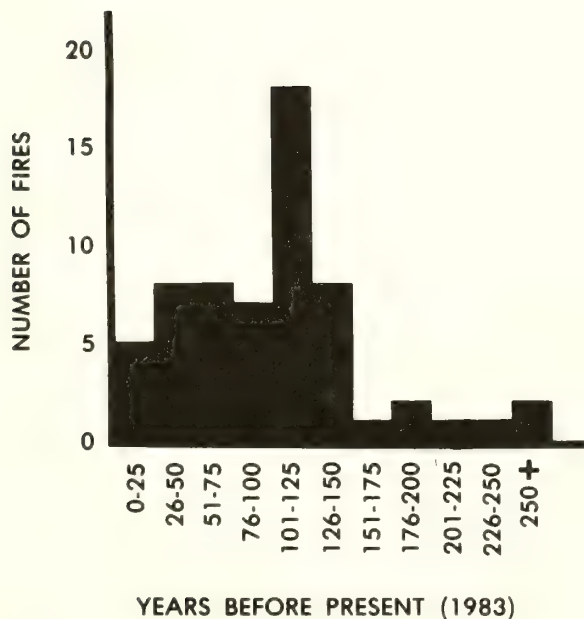


Figure 3.--Number of fires during 25 year periods in Taylor Park, Colorado as determined from scarred lodgepole pine trees.

at least 133 years. Lodgepole pine forests are considered to have a variable fire regime consisting of frequent, low-intensity surface fires and infrequent, high-intensity stand destroying fires (Kilgore 1981). The fire return intervals reported here approximate such a fire regime although some return intervals are lower than reported by other authors (Arno 1980). The number of fires that occurred during the life of each stand ranged from one to eight. Over half the stands had been burned at least four times during their life span (table 1). Fire frequency, expressed in fires per year, was extremely low, although the highest was nearly 20 times greater than the lowest frequency (table 1).

Relationships Between Dwarf Mistletoe Infection and Fire History

In figure 4, DMR is plotted against the mean fire return interval. Superimposed on this figure is a line which represents the rate of dwarf mistletoe intensification over time. This line illustrates the relationship between DMR and time since infection presented by Hawksworth and Hinds (1964). This relationship is plotted on this figure because it was expected that a plot of DMR versus the mean fire

return interval would have data points clustered about this line. However, this was not the case; data points are scattered over the graph. Interpretation of this figure in terms of the time since infection and time since the last fire does, however, provide a possible explanation for some of the variation. Those stands where dwarf mistletoe infection has been present longer than the time since the last fire represent situations where the most recent fire did not eradicate the parasite from the stand. Consequently, DMR escalation during the subsequent fire-free period appears very rapid. In those stands infected since the last fire, the disease has probably spread from outside the stand and these points are scattered around the projected rate of DMR intensification over time. Two stands plotted in the upper left-hand corner of the figure, however, are not accounted for by either of these explanations.

The mean fire return interval merely reflects an arithmetic average. Some very long return intervals in combination with very short intervals could yield a misleading average. So, mean fire return intervals appear limited in their usefulness for relating dwarf mistletoe infection history to fire history. This fact was borne out during linear regression analyses of these data which produced an equation with $R^2 = .13$. Length of time from the last fire in combination with the most recent fire return interval may be more informative when attempting to relate dwarf mistletoe infection history to fire history.

The intensity with which a fire burns is directly responsible for the type of post-fire infection source (ie, even, uneven, or peripheral (Baranyay 1970)), and can both encourage and discourage dwarf mistletoe spread and intensification (Hawksworth 1969). High intensity fires that consume all or nearly all of a stand, causing simultaneous death of all infected trees and parasite plants, tend to discourage dwarf mistletoe development and spread. Following this type of fire a sanitized stand results in which the reinventing tree regeneration develops at a faster rate than the parasite (Jones 1974). On the other hand, fires that burn sporadically

permit the survival of infected trees (even or uneven infections) which spread the pathogen to regeneration and encourage dwarf mistletoe intensification (Kimmey and Mielke 1959, Graham 1960, Hawksworth 1969, Muir 1970). If fires kill all trees in a single stand but leave surrounding infected stands undisturbed, then peripheral infections occur. In these instances, the pathogen would be expected to increase at a rate somewhere between the two previously mentioned extremes.

The role of fire in encouraging or discouraging dwarf mistletoe is clearly illustrated when DMR is plotted against time since the last fire, with the relationship between parasite intensification and time since infection again plotted as a line (fig. 5). Those points above the line represent stands where fire has encouraged dwarf mistletoe intensification. Incomplete consumption of infected trees permitted reinfection of regeneration and rapid escalation of the DMR. Those points below and to the right of the intensification line represent stands where fire has discouraged dwarf mistletoe. In these stands, high intensity fires have probably killed all infected trees and effectively eradicated the disease. Spread from surrounding infection centers has been slow. Immediately adjacent to the intensification line are those stands where fire was responsible for removal of dwarf mistletoe, and reinfection progressed steadily from peripheral infection sources.

If fire occurrence is important in dwarf mistletoe regulation, then increasing fire frequency should result in decreasing DMR levels. The relationship for the Taylor Park stands is illustrated in Figure 6. Dwarf mistletoe rating clearly decreases as fire frequency increases. Linear regression analysis yielded the following equation for predicting DMR from fire frequency:

$$DMR = 5.485 - 79.574 * (\text{FIRE FREQUENCY})$$

This equation accounts for 47 percent of the variation among the sampled stands and is plotted in figure 6.

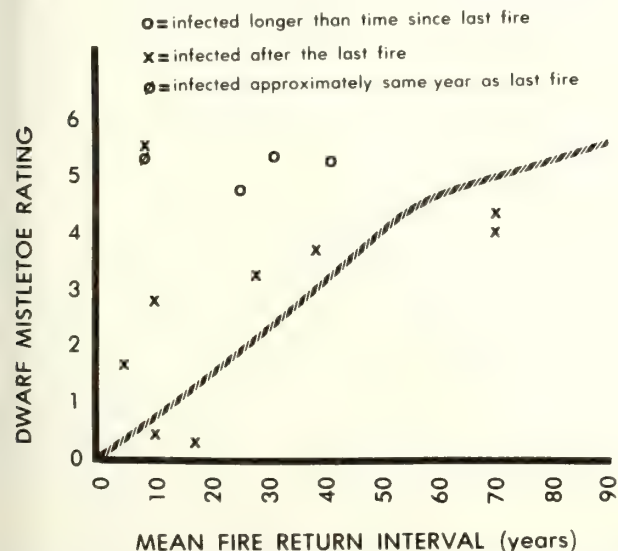


Figure 4.--Relationship between average stand dwarf mistletoe rating and mean fire return interval.

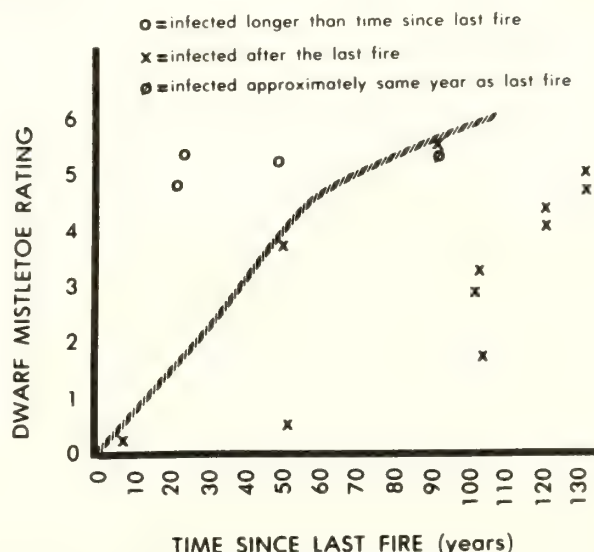


Figure 5.--Relationship between average stand dwarf mistletoe rating and time since the last fire.

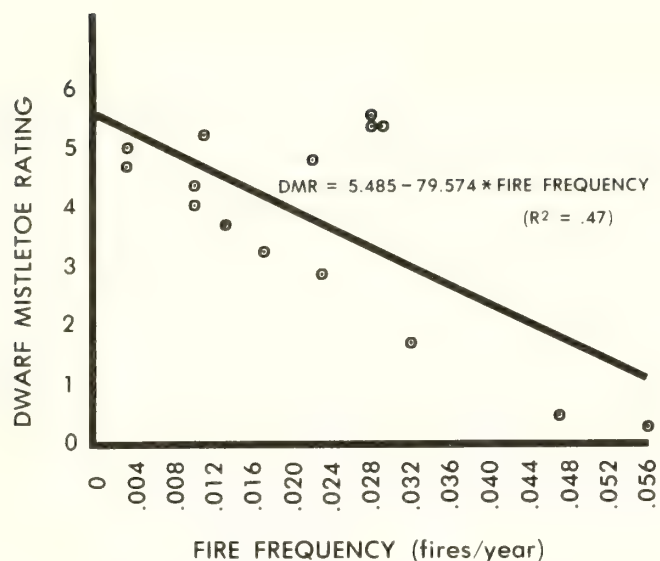


Figure 6.--Relationship between average stand dwarf mistletoe rating and fire frequency.

Effects of Fire Exclusion on Dwarf Mistletoe Spread and Intensification

Fire exclusion effects on dwarf mistletoe spread and intensification are not well understood (Brown 1975). A policy of wildfire suppression is thought to have removed the only natural control and facilitated an increase in dwarf mistletoe in lodgepole pine forests during the past few decades (Kimmey 1957; Baranyay 1970, 1975; Heinselman 1970; Smith and Baranyay 1970; Loope 1971; Hawksworth 1975). However, in those stands where shade tolerant species succeed lodgepole pine, fire exclusion could indirectly reduce dwarf mistletoe infection by reducing the numbers of lodgepole pine and increasing the numbers of shade tolerant individuals (Bloomberg 1950, Brown 1975). Since most of these shade tolerant species are immune to lodgepole pine dwarf mistletoe (Hawksworth 1975), a decrease in infection centers will result.

Within lodgepole pine forests fire behavior cycles are believed to follow definite trends (Muraro 1971, Brown 1975, Van Wagner 1983). Lodgepole pine fire intensity potential which refers to fire growth and heat release potential, is illustrated over time in figure 7 (Brown 1975). The most frequent occurrence believed to occur in these stands is shown by curve A. Young stands, especially dense ones, possess the greatest fire potential while moderately dense to open advanced immature and mature stands have the least fire potential (Muraro 1971; Brown 1975; Van Wagner 1977, 1983). Potential fire intensity increases rapidly to a maximum during the initial 20-30 years of stand development, although intense fires are possible in forests as young as 10 years (Van Wagner 1983). Potential fire intensity then decreases until stand deterioration where it again increases (Muraro 1971, Brown 1975, Van Wagner 1983). Curve C represents situations where surface fuel quantities and fire potential remain relatively low throughout the life of the stand until decadence (Brown 1975). Potential fluctuation between these

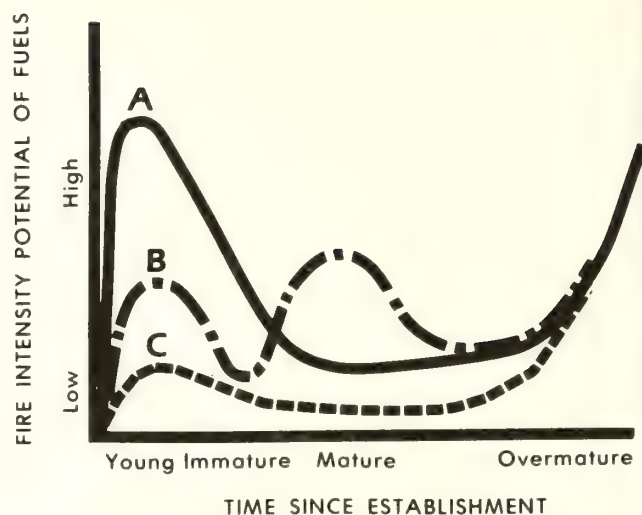


Figure 7.--Fire intensity potential cycle in lodgepole pine forests (Brown 1975).

two curves during younger ages and prior to increase fire intensity at later ages is illustrated by curve B (Brown 1975).

Thus, if a regular trend in fire behavior potential exists in lodgepole pine stands, it is likely that a similar trend in the number of fires also exists. Maximum numbers of fires probably occur during periods when a large percentage of stands have reached the most hazardous stages. This trend is apparent for stands in the Taylor Park area (fig. 4). Fire occurrence, derived from fire-scarred trees, increased from 1723 to a peak between 1858 and 1892 and then decreased. If dwarf mistletoe presence is related to fire occurrence, then dwarf mistletoe frequency should be at a minimum shortly after the peak of fire occurrence. Number of fires or number of stands burned and percent of stands infected by dwarf mistletoe for Taylor Park lodgepole pine stand are plotted for 10 year periods from 1713 to 1983 in figure 8. The pattern of fire occurrence subdivided into 10 year intervals appears to further substantiate a fire cycle for this area. In addition, in 1983 10 percent of the sampled stands were infected by dwarf mistletoe while approximately 95 years ago, none of these stands were infected. This minimum in the frequency of dwarf mistletoe infection lags slightly behind the peak years of fire occurrence.

If lodgepole pine stands in the Taylor Park area are subject to a fire occurrence cycle, then, during the twentieth century, fire occurrence has followed a decline in response to declining stand fire behavior potential. Consequently, dwarf mistletoe infection intensity and frequency have followed a cyclic increase which will persist until the next peak in fire occurrence.

Although the effects of fire suppression have not been as serious in these lodgepole pine stands as previously believed, continued fire exclusion could have serious ramifications. These lodgepole pine stands now have a very high percentage of dwarf

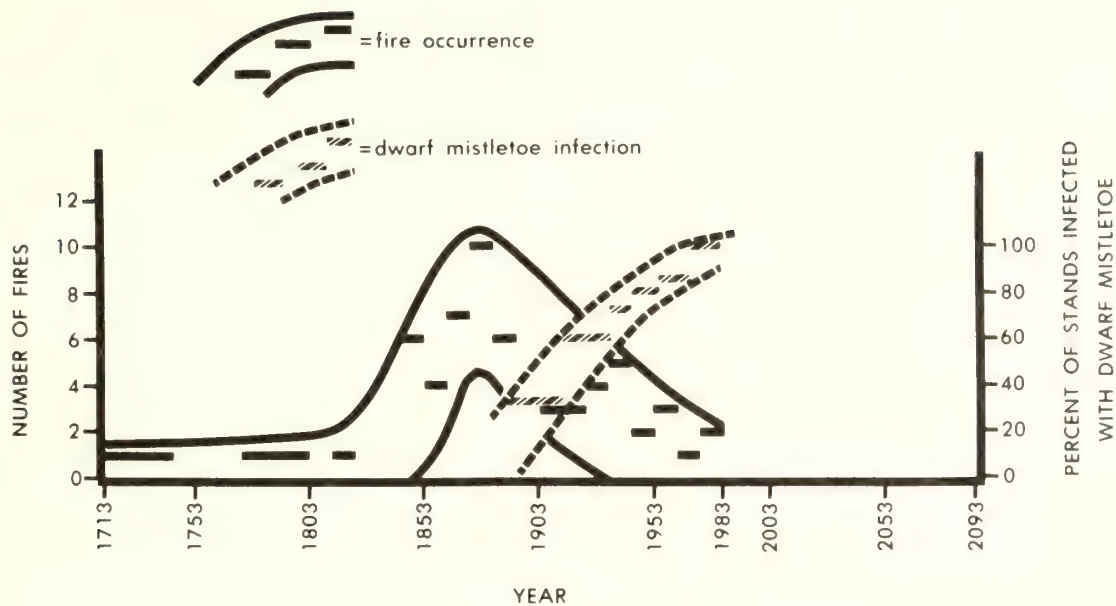


Figure 8.--Fire and dwarf mistletoe dynamics in lodgepole pine stands of Taylor, Colorado.

mistletoe infection. A continuation of the fire suppression policy in the absence of alternative dwarf mistletoe control or eradication methods will permit continued parasite spread and proliferation and drastically reduce stand productivity. In addition, continued fire suppression could decrease the number of stands of different ages and the large number of young stands usually associated with fire-dependent forests. A mosaic of few rather than many age classes will result where a large percentage of stands will reach a stage of high potential fire intensity at the same time which could drastically affect forest protection problems.

SUMMARY

The relationship between fire and dwarf mistletoe is difficult to quantitatively document. But in lodgepole pine stands in the Taylor Park area of southwestern Colorado certain trends are apparent. Fire frequency appears to be more useful than either mean fire return interval or time since the last fire for relating dwarf mistletoe infection intensity to fire history. Average stand dwarf mistletoe ratings of lodgepole pine stands in Taylor Park are inversely proportional to the fire frequency recorded in fires per year. The usefulness of this relationship should, however, be interpreted with caution. This study indicates lodgepole pine stands in Taylor Park, Colorado are subject to a variable fire regime: longer interval stand destroying fires superimposed on more frequent fires of lesser intensities. Areas outside the limits of this study could be subject to far different fire regimes where the relationship between dwarf mistletoe infection and fire history is unlike that reported here.

Wildfire suppression over the past few decades in lodgepole pine stands in Taylor Park, Colorado has not resulted in increased dwarf mistletoe

infection intensity and frequency. The increase that has occurred is instead a predictable result of the dwarf mistletoe and fire dynamics of this area. But, continued fire suppression in these lodgepole pine stands, in the absence of alternative dwarf mistletoe controls, will permit dwarf mistletoe to continue to spread and intensify. Ultimately, severe losses in stand productivity will occur.

Because of its parasitic nature, dwarf mistletoe is adversely affected by any factor that harms host trees. Lodgepole pine stands in the Taylor Park area are strongly influenced by wildfire occurrence. Fire represents one of the foremost natural agents of dwarf mistletoe regulation and influences parasite presence and abundance through affects on both the parasite plants and lodgepole pine hosts.

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The dwarf mistletoes are the most damaging group of parasitic seed plants in North America. This symposium concentrated on their basic biology, with 16 papers summarizing current world research on various fields, including ecology, biosystematics, evolution, cytogeography, host-parasite physiology, and anatomy of the parasite root system.

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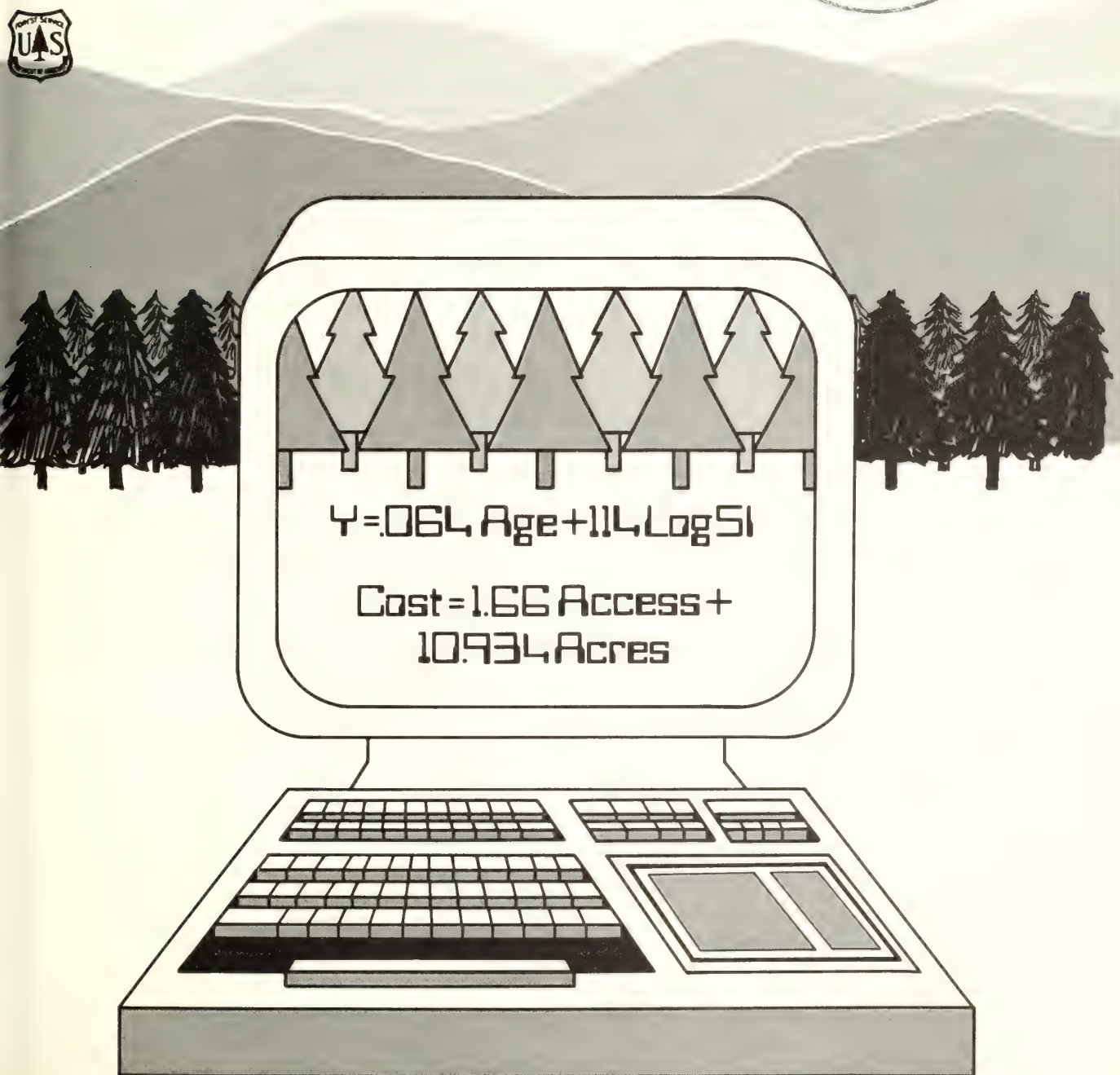
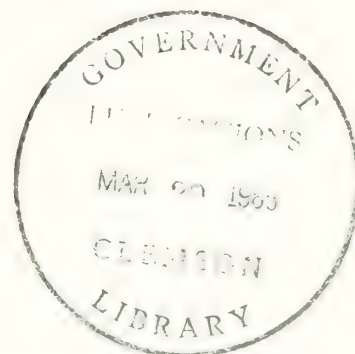
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General Technical
Report RM-112



Regional Timber Yield and Cost Information for the South: Modeling Techniques

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J. Michael Vasievich



Abstract

This report surveys analytical techniques for estimating the timber production of southern forests under various forestland management alternatives, and associated costs of those management alternatives. The integration of information from growth and yield modeling with timber management cost information in regional timber studies also is examined. Appendixes summarize the nature of data used to develop the timber growth and yield models, inputs required and outputs provided by the timber growth and yield models, and availability of cost information for different forestland management practices.

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The authors appreciate the help and advice of Richard W. Guldin, Economist, USDA Forest Service, Southern Forest Experiment Station, New Orleans, La.

Regional Timber Yield and Cost Information for the South: Modeling Techniques

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Contents

	Page
INTRODUCTION	1
BACKGROUND	2
MODELS OF TIMBER GROWTH AND YIELD	3
EVALUATION CRITERIA	3
DIRECT METHODS	4
INDIRECT METHODS	4
Whole Stand Models	4
Diameter Distribution Models	5
Individual-Tree Models	5
Distance-Independent Models	6
Distance-Dependent Models	6
GROWTH AND YIELD INFORMATION BY FRES ECOSYSTEM AND TIMBER TREATMENT CLASSES	7
GENERAL COMPARISONS OF TIMBER PRODUCTION MODELS	7
COST INFORMATION	8
ACCOUNTING/SURVEY APPROACH	8
ENGINEERING/DELPHI APPROACH	9
STATISTICAL APPROACH	9
INTEGRATION OF PRODUCTION AND COST INFORMATION	11
OVERVIEW AND CONCLUSIONS	12
LITERATURE CITED	13
APPENDIX 1. Summary of Timber Growth and Yield Models Surveyed	19
APPENDIX 2. Selected Characteristics and Nature of Data Used in Timber Growth and Yield Models	20
APPENDIX 3. Inputs and Outputs for Timber Growth and Yield Models ...	24
APPENDIX 4. Cost Studies for Timberland Treatments	28

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INTRODUCTION

Both the public and private forest sectors utilize analyses of regional timber supply trends in formulating forest management policies. In past analyses, most of the projected increase in U.S. timber product output in the next several decades is based on southern timber resources (USDA Forest Service 1982). The potential responses of timber stands to a wide variety of different land management regimes are essential information elements in these regional timber supply analyses.

This report surveys (1) methods for predicting southern timber production under different management alternatives, and (2) the economic costs of management alternatives. These analysis techniques have been developed primarily for use at the stand level. Estimates of regional timber productivity involves balancing loss of relevant detailed information in aggregation with "costs of detail." Both biological and economic information is needed to estimate the economic costs of producing different amounts of timber. These cost functions can help explain how the amount of timber supplied by timber owners is influenced by different levels of economic incentives (e.g., stumpage prices, government subsidies).

The report is intended primarily as a reference document for regional timber supply analysts. It provides a review of major analytical techniques useful in long-range studies of southern timber supplies and expands on a brief presentation of timber inventory projection models by Alig et al. (1984).⁴ This report summarizes information useful in analyzing the timber growth and yield and associated management costs in the South. Several related surveys have been published (Burkhart 1975, 1981; Farrar 1979b); however, these do not include management costs. Annotated bibliographies of general growth and yield information (i.e., not limited to yield projection methods) are also available for the major southern pines (Williston 1975) and southern hardwoods (Miller 1967, 1974), but they also do not address the complete set of biological and economic data required in timber supply analysis.

⁴A related survey of timber growth and yield models is given in the following report: Parks, Peter J. 1982. Survey of analytical techniques for estimating southern forest production possibilities. Final report for USDA Forest Service Contract PO 43-82LM-2-72, 63 p. Copy on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Regional timber supply analyses examine a broad range of complex biological and economic interrelationships at coarse aggregate levels. The FRES ecosystem classification (Garrison et al. 1977) has been used to classify approximately 188 million acres of commercial forestland in the South by cover type (table 1). Approximately 50% is in the southern pine and oak-pine types, and the majority of the remainder (31%) is in the oak-hickory type. Forest management activities, including site preparation, regeneration, intermediate stand treatment, and harvest activities, were performed on 3.3 million acres in 1978 (NFPA 1980). In addition, more than 100 million acres of private, commercial forestland in the South were estimated capable of returning a real rate of return of 4% or more if certain management practices are applied (USDA Forest Service 1981b).

Management practices considered here were identified in the 1980 Resources Planning Act (RPA) Assessment (USDA Forest Service 1981b). Panels of forestry experts in each state identified opportunities for economic investments in forest management (in addition to those expected to be completed under the perceived current level of management). Five groups of investment opportunities were identified according to the type of timber treatment that was needed (table 2). The classes of management considered for the midsouth region (Alabama, Arkansas, Louisiana, Mississippi, Oklahoma, Tennessee, and Texas) were softwood opportunities: density control, regeneration of nonstocked acres, and

Table 1.—Area of southern commercial forestland classified by FRES ecosystem¹

FRES no.	FRES ecosystem	Area	
		thousand acres	percent
10	White-red-jack pine	370.3	0.2
11	Spruce-fir	7.9	0.0
12	Longleaf-slash pine	16,754.7	8.9
13	Loblolly-shortleaf pine	46,576.0	24.8
14	Oak-pine	30,469.7	16.2
15	Oak-hickory	58,939.1	31.3
16	Oak-gum-cypress	26,062.3	13.9
17	Elm-ash-cottonwood	3,243.3	1.7
18	Maple-beech-birch	424.7	0.2
	Nonstocked	5,197.8	2.8
Total		188,045.8	100.0

¹Based on USDA Forest Service (1982) data.

Table 2.—Definitions of timber treatment classes utilized in regional investment opportunity analysis in 1980 RPA Assessment

Treatment class	Generalized definition
Density control	Represents a broad group of silvicultural options often referred to as "intermediate stand treatments." In general, the class includes precommercial thin, prescribed burn, clean, release, and commercial thin. Certain areas of the country added specific variations. Minor variations were reflected throughout the U.S., but the underlying goal was some managerial treatment that would improve the residual stand of hardwoods or pines to enhance volume and value growth.
Stand conversion	Reflects decisions to harvest or clear existing stands of low-value or low-growth hardwoods and replace them with favored coniferous species. Selection of a method of regeneration depended upon the availability of desirable advance reproduction or a natural seed source, but in most cases resulted in recommendations to clear, site-prepare, and plant.
Regenerate nonstocked land	Nonstocked land is defined as commercial forestland less than 16.7% stocked with growing-stock trees. Recommended treatments of these acres throughout the country was to site prepare and plant the appropriate coniferous species for the geographic region.
Harvest and regenerate hardwoods	Recommendation includes harvest of mature bottomland stands of hardwoods in the Southeast with site preparation for natural regeneration.
Harvest and regenerate softwoods	Harvest and regeneration of mature and over-mature softwood stands. Method of regeneration selected depended on availability of seed source and present-net-worth comparison of natural and artificial regeneration. In most cases, artificial regeneration provided higher present net worth.

Source: USDA Forest Service (1981b).

harvest and regeneration of existing stands. The softwood treatment opportunity classes for the Southeast region (Florida, Georgia, North Carolina, South Carolina, and Virginia) were density control, stand conversion, regenerating nonstocked acres, and harvest and regeneration of existing stands. The hardwood treatment opportunity in the Southeast was regeneration to hardwoods.

Nontimber forestland management practices are not directly considered in this report; however, responses of timber stands to nontimberland management practices can be modeled, in some cases, if the management practice can be translated into effects on timber growth and yield parameters (e.g., reduction in basal area). The only forest output considered in this survey is timber. Nontimber forest products and services are produced by forestland management; but, separating the individual costs (per output category) in a variable joint production process is not theoretically tenable (Hof 1983). In addition,

supporting data pertaining to technical production relationships among inputs and outputs for nontimber resources are quite limited.

Only the costs of different levels of inputs utilized in land management practices that were reported in the literature are considered here. While this includes mixture of variable and fixed costs, it is by no means complete set of management costs. Harvesting costs are not discussed in this report. See Cubbage and Gransko (1982) and McCollum and Hughes (1983) for recent examples of related studies.

BACKGROUND

The economic framework for timber production involves principles that affect, condition, and control (1) the response of forestland to varying combinations of capital and labor inputs; and (2) the economic return that accrue to timber-producing forestland after payment of wages and interest to labor and capital. Examination of southern timber production potentials in the context of timber production economics requires a broad understanding of the underlying biological and economic fundamentals. Marginal costs of supplying different quantities of stumpage depend largely on the underlying productivity of the land and the timber management practices applied. Forest product values are required for the estimation of economically efficient levels of timber production, but reviewing studies on these topics is outside the scope of this report. For information on regional timber values, see Adams et al. (1979), Adams and Haynes (1980), Neal and Kennen (1981), USDA Forest Service (1981a), and Wallace and Silver (1981).

The production of timber from forests has been modeled as a neoclassical economic production function (e.g., Hyde 1980, Nautiyal and Couto 1982). From this perspective, management intensity and site quality are important determinants of timber production, although the latter factor is not always identifiable as an input in an economic sense. Associated input costs can be separated into two broad categories: (1) payments to factors of production (e.g., management costs); and (2) the opportunity costs of keeping the land in timber production (Hyde 1980). The relationship between input costs and output values determines the economically efficient management regime (Anderson 1972).

Traditional timber growth and yield models have been viewed as production functions whose only discretionary input is time. These are typically adjusted for site productivity via some productivity index. Most existing information pertains to unmanaged even-aged stands of pine, although some yield functions for uneven-aged stands have recently been reported (Farrar et al. 1984). Empirical growth and yield models can be used to develop economic production functions, which can in turn be used to analyze economically efficient timber production.

Nautiyal and Couto (1982) analyze output-input relationships using elasticities. The elasticities of output with respect to various inputs provide a measure of

their individual contributions to the timber production process. Elasticities of scale describe the relative increase in timber output attributable to a proportional increase in all inputs. Output-input relationships, as measured by elasticities of substitution, characterize the curvature of production function isoquants, and indicate the relative ease with which inputs can be substituted for each other. For example, Adams et al. (1982) suggest that the South has significant opportunities for increasing growth through intensive management. One method of quantifying these increases could be to analyze the relevant elasticities.

Both physical growth and yield for different sites, species, and management practices (e.g., yield change after fertilization) and the costs of such practices must be estimated, as demonstrated by Vaux (1954, 1973) in an earlier analysis of timber-growing potential in California. Considerably more published information is available on the growth and yield of timber than for the associated costs of management practices. Nevertheless, costs of production are a crucial consideration when estimating the quantity of timber supplied by timber owners in response to economic incentives. Given the input and output relationships for a particular forest type and site class, assigning costs to the inputs permits estimation of costs for different output levels. For example, Vaux (1973) calculated the aggregate amount of timber that could be grown at or below various maximum average costs per unit of output.

MODELS OF TIMBER GROWTH AND YIELD

Models of southern timber growth and yield have evolved from yield tables for fully stocked, unmanaged, natural stands to computerized models that are applicable to a wider range of stand density regimes and management practices. As models evolved, the methods used to project future timber inventories (growth, mortality, accumulated stock, and structure) in the South (Alig et al. 1984) have changed. When comparing alternative growth and yield models, a useful approach is to first separate the models into two broad classes—direct and indirect methods. Direct methods are applied locally to the same stand from which the data used for projection purposes are obtained. In contrast, indirect methods develop estimates from a sample set of stands and interpolate relationships found for other stand conditions within the bounds of the sample set (Davis 1966). These methods will be reviewed after evaluation criteria have been discussed.

EVALUATION CRITERIA

Specific criteria for evaluating the usefulness of southern timber growth and yield models in regional timber supply analyses are not readily discernable from the literature. Before specific evaluation criteria can be applied, the objectives or goals and the associated information needs of regional timber supply analyses must be defined. Two general evaluation criteria have been ap-

plied in this report: (1) extrapolation or flexibility, and (2) validation. These two categories are central to a model's applicability.

Extrapolation considerations include the appropriateness of the growth and yield relationships for use in constructing area-specific variants of the model. The range of data used to construct a model (e.g., ages, density levels) is a particularly important consideration because extrapolation beyond the range may result in inaccurate prediction by the model components (e.g., site index curves, tree volume equations). Appendix 2 provides the reported ranges and limitations of southern growth and yield models.

Validation criteria of growth and yield models are more quantitative than the evaluation criteria. However, the completeness and consistency of validation procedures and results are far from ideal. Validation of long-range timber production models has received limited discussion in the literature. In particular, the importance of accurate representation of real-world timber growth and yield processes or systems has not been adequately discussed. Few articles have described the accuracy of any model in detail. Furthermore, articles about validation of simulation techniques are often philosophical in nature rather than containing practical recommendations or guidelines (Law and Kelton 1982).

Major validation considerations include the following:

1. The data used to validate the model should be independent from data used to develop the model.
2. The model should be validated on the basic outputs it produces. For example, a model that produces diameter-class attributes should be validated on the diameter-class attributes, rather than aggregated stand attributes.
3. Statistical residuals of the validation data set should be similar to those generated by the original data set.
4. Trends in model predictions should follow trends in the validation data set.
5. The model should not exhibit a large amount of bias (i.e., predictions should not be consistently above or below the validation data) (Hann 1980).

In general, test statistics relating to the development of the model (e.g., statistical significance of predictor variables) in most growth and yield studies are not given. Several past studies have required that all variables included in an equation be above a given significance level. Validation results are most commonly presented in terms of mean differences between actual and predicted values. Bias is frequently examined by testing the statistical hypothesis that mean difference is zero. Plot selection criteria usually lead to slight positive bias, with yield predictions representing potential yield rather than actual yield. Most studies provide information on the "fit" of the equations to the data (e.g., multiple correlation coefficient (R^2), standard error of estimate).

These two categories of evaluation criteria provide some broad guidelines for judging model performance. They are not comprehensive criteria that would support

a critical examination. Because each timber supply analysis has its own specific objective, evaluation of specific growth and yield projection methods cannot be rigorously pursued in this review.

DIRECT METHODS

Direct methods of growth and yield projection techniques involve analysis of a particular stand in terms of measured variables (Davis 1966, Avery and Burkhart 1983). The most familiar direct method is stand table projection, in which a sample of growth rates is obtained and applied directly back to the same stand to project growth. Stand tables are composed of frequency data showing number of trees classified by species, diameter at breast height (d.b.h.), or height. Stand tables, commonly expressed on a per-acre basis, depict the stand structure or distribution of tree sizes and species in a stand. Stand table projection models use estimates of future diameter growth, removals, mortality, and ingrowth to adjust the stand table over time.

Direct methods have typically been used to address localized, individual-stand development questions in the South. An exception is application of the stand table projection approach in the Timber Resource Analysis System (TRAS) (Larson and Goforth 1970, Alig et al. 1982), which has been employed in regional and national timber assessments. To answer these broader aggregate stand- or forest-level questions, the assumption is made that a large, regional inventory can be treated as one all-aged stand. The TRAS model is based on an exponential size class distribution, the Q-method, to simulate the growth of large aggregations of individual even-aged and uneven-aged forest stands (Larson and Goforth 1974).

The TRAS model was not designed to accommodate timber management shifts required in recent timber supply studies (Alig et al. 1984), especially changes in management intensity by age classes for the even-aged types in the South (i.e., changes in region-wide age structure). The TRAS model combines treated and untreated forest acreage to attain weighted average acres; this precludes modeling the response to individual timber treatments by specific age classes or other strata (i.e., all acres are treated equally). A package of timber treatments is assumed to be applied across all "average" acres in an ownership aggregate (e.g., softwoods on nonindustrial lands in the Southeast), phasing them in over time by adjusting radial growth increments for each diameter class over a simulation period (Barber 1980). In this aggregate approach, the total growth increment to be phased in is taken from the RPA regional investment opportunity analysis (USDA Forest Service 1981b).

Other models that are designed for a more disaggregated or detailed approach include the Timber Resource Inventory Model (TRIM) (Tedder 1983). Forest acreage in TRIM is stratified by age classes and descriptions for ownership, site, species, and stocking level. Yield tables (e.g., McClure and Knight 1984) constructed for dif-

ferent levels of timber management or investment for these strata are basic inputs into the TRIM systems.

The Southern Pine Age-class Timber Simulator (SPATS) developed by Brooks (1984) for the Southeast and South-central regions is an investment-sensitive age-class model with a level of aggregation that is intermediate between the TRAS and TRIM approaches. SPATS models three different softwood-related types: (1) pine plantations, (2) natural pine, and (3) oak-pine. One average site class is employed for each type. The softwood timber inventories in the South are projected separately for two private owner groups—forest industry and other private—in 5-year intervals. Investment functions in the SPATS model, driven by market forces and government policy actions, select timber management practices to be simulated to allow evaluation of the effect of cost-share payments on future timber supplies and prices.

INDIRECT METHODS

With the advent of large, high-speed computers several sophisticated methodologies are now used to predict timber production. The most widely used techniques are whole stand models, diameter distribution models, and individual-tree models. Examples of each type of model are listed in appendix 1. Information on data used to develop these models and the resultant outputs are provided in appendixes 2 and 3.

Whole Stand Models

In the whole stand approach, aggregate stand volumes are projected from stand-level variables such as age, site index, or basal area per acre. Usually, no information is provided on volume distribution by size class but in a few cases merchantable, sawtimber, and pulpwood volumes can be estimated. Since the original work by MacKinney and Chaiken (1939), multiple regression techniques have been used frequently. Most of the available models are of this type, especially for natural stands. The computational simplicity of most whole stand models allows rapid execution on computers.

The introduction of "compatible" growth and yield models was a major development in whole stand modeling. A growth model is compatible with a yield model when yield may be obtained through mathematical integration of growth over time. Clutter (1963) developed compatible models for cubic foot volume growth and yield in loblolly pine. Sullivan and Clutter (1972) later revised Clutter's models in an attempt to overcome two statistical problems: (1) dependent parameters within a system of equations; and (2) nonindependent observations from remeasured plots. They simultaneously estimated current and future stand volume as a function of initial stand age, initial basal area, site index, and future age. Brender and Clutter (1970) first applied this simultaneous estimation technique.

Further refinements in parameter estimation techniques for compatible or simultaneous models include development of such cubic foot volume and basal area projections by Burkhart and Sprinz (1984) and Murphy (1983). Compatible models have also been developed for slash pine (Bennett 1970, Matney and Sullivan 1982), shortleaf pine (Murphy and Beltz 1981, Murphy 1982), longleaf pine (Farrar 1979a), and yellow-poplar (Schlaegel and Kulow 1969, Beck and Della-Bianca 1972). With a few exceptions for thinned plantations (Sullivan and Williston 1977, Lohrey 1979, Matney and Sullivan 1982, Bailey and Ware 1983, and Burkhart and Sprinz 1984), compatible models developed to date are for thinned natural stands. Current stand volume is predicted from age, site, and basal area (i.e., density). Future basal area is predicted from present basal area, present age, and future age, and, sometimes, site index. An equation to predict future volume is obtained by substituting the future basal area equation and future age in the original volume equation.

Whole stand models that provide yield estimates for a variety of units of measure or merchantability standards frequently develop volume ratios to convert a basic yield to various forms. Occasionally (Beck and Della-Bianca 1975, Farrar 1979a, Murphy 1982) these ratios were developed separately to supplement existing models (Beck and Della-Bianca 1972, Farrar 1979a, Murphy and Beltz 1981, respectively). Typically, either volume ratios, basal area ratios, or volume-basal area ratios are dependent variables predicted from stand-level variables relating to the age, basal area, volume, and sometimes, site index of the stand or tree size. With a few exceptions (Bennett et al. 1959; Burkhart et al. 1972a, 1972b; Goebel and Warner 1969), whole stand models also provide future basal area estimates.

Diameter Distribution Models

Similar to the whole stand approach, the diameter distribution approach uses information typically collected in a conventional inventory (age, site, and density). However, this approach can deliver information for any stand table fraction, up to the whole stand. Diameter distribution models are useful for multiple-product analyses because they provide information by diameter classes. For example, Bennett and Clutter (1968) developed multiple-product (sawtimber, pulpwood, and gum) yield tables for slash pine plantations. Almost all diameter distribution models currently available are for pine plantations (appendix 1); exceptions are the Beck and Della-Bianca (1970) and Schreuder et al. (1979) models for natural stands of yellow-poplar and slash pine, respectively.

For the diameter distribution technique, parameters of a probability density function (PDF) are estimated from stand characteristics. The relative frequency distribution of diameters within the stand is used with total frequency to construct a stand table (i.e., tree frequency table by diameter class). The typical sequence of events is: (1) average tree heights are predicted for each diameter class; (2) average volume per tree is calculated

using a tree-volume equation or integrated stem profile function; (3) volume per class is calculated using volume per tree and trees per class. Aggregate volume for any fraction of the stand can be calculated by summing the appropriate diameter classes. Projections through time can be made by estimating future diameter class density (i.e., trees per acre) and repeating the process. Compatible growth and yield models have also been developed using the diameter distribution method (e.g., Strub et al. 1981).

The key difference between diameter distribution models is in the PDF used to describe the diameter distribution. Initial applications of this technique used the beta PDF (Bennett and Clutter 1968, Lenhart and Clutter 1971, Lenhart 1972, Burkhart and Strub 1974). Most recent applications have used either the Weibull PDF (Clutter and Belcher 1978, Dell et al. 1979, Feduccia et al. 1979, Lohrey and Bailey 1977, Matney and Sullivan 1982, Smalley and Bailey 1974a, 1974b), or the Johnson S_B (Hafley and Schreuder 1977), S_{BB} (Schreuder and Hafley 1977), or S_{BBB} (Schreuder et al. 1982a, 1982b) PDF's.

Computational procedures for diameter distribution models are relatively efficient. In a study by Daniels et al. (1979b), execution time on a computer for the Burkhart and Strub (1974) diameter distribution model was 0.25 seconds per stand estimate. Execution times for the whole stand model (Burkhart et al. 1972b) and the individual tree model (Daniels and Burkhart 1975) were 0.01 and 13.78 seconds, respectively.

Versatile tree volume-defining equations, or integrated stem profile functions, used in the diameter distribution approach provide an opportunity to diversify the outputs from these models. Yields per tree can be obtained in any units (e.g., board feet, cords, dry weight, etc.) inherent in tree-volume functions. It is often possible to use several different tree-volume equations or a stem profile function to obtain volume estimates in a variety of units of measure. Most diameter distribution models are capable of producing basal area estimates for any fraction of the stand because tree frequency by diameter class is known or estimated.

Burkhart (1971) evaluated the accuracy and precision of the diameter distribution yield estimation for old-field slash plantations developed by Bennett and Clutter (1968) through an independent sample in south Georgia and north Florida. He concluded that, for large samples, yields of old-field slash pine plantations can be reliably predicted by the Bennett-Clutter technique. Variation of individual plots may be relatively large, but on the average the technique gives accurate results.

Individual-Tree Models

A common characteristic of the variable density growth and yield models discussed above is their reliance upon aggregate stand or size class characteristics such as basal area or number of trees for modeling of forest development. The most recent approach for modeling forest growth and yield is use of individual-tree simulation models. Stands are described

on the basis of characteristics of individual trees, which are then combined to form stands. These models consider a set or list of individual trees and associated tree or stand characteristics for a plot. They simulate the growth of each tree by explicit or implicit "potential" growth functions; these, in turn, are modified by expressions reflecting competition due to number and size of associates (Ek 1977). In this manner, tree spatial locations and individual tree characteristics influencing tree growth and yields may be explicitly considered. There are two general classes of individual-tree models: (1) those that do not require intertree distances, and (2) those that require intertree distances as a necessary input (Munro 1974).

Distance-Independent Models

Individual-tree distance-independent models classify the competitive status of the subject tree by comparing its characteristics (size, crown ratio, etc.) in relation to all other trees in a sample plot. Each sample tree is weighted with an expansion factor—the number of trees per acre it represents.

The advantages of this type of model are that it can be used for any age structure or species mixture and it provides relatively detailed information on tree and stand parameters and on the effects of stand management. Disadvantages include its relative complexity and the inability to predict the growth of specific single trees with high reliability (Munro 1974). All of the individual-tree models described herein are similar because they involve some type of tree accounting, product conversion, and summary capability. Actual stand dynamics are also simulated by specific program sections or subprograms for survivor tree growth, mortality, and, sometimes, ingrowth or regeneration. There may also be subprograms for management activities, such as harvesting or thinning. Specific options for insect and disease impact studies and habitat analyses have also been developed.

Individual-tree distance-independent models have been employed to simulate growth and yield for individual forest stands, small forested areas, and for entire states in other parts of the country (Alig et al. 1984). Aggregation capabilities of these models, potential costs of adapting them to large-scale assessments, the number of plots needed to represent forest conditions in regional timber assessments, and model validation require further examination (Alig et al. 1984). An individual-tree model capable of projections for 20 species may be no more complex (and probably less so) to construct and use than 20 "simpler" models for 20 different species.

No individual-tree distance-independent models for southern forest types have been reported in the literature. One proposal is the calibration of the Stand and Tree Evaluation and Modeling System (STEMS), formerly known as the Forest Resources Evaluation Program (FREP) (USDA Forest Service 1979, Moeur and Ek 1981) for use in the South. STEMS is an individual-tree distance-independent model designed to describe stand

development, with or without management activities. STEMS can be used to update or project stand development or to evaluate various silvicultural management alternatives. The model has several timber management options available. The model's timber growth projection system has been applied in the Lake States (Jakes and Smith 1980) and can model a variety of forest conditions including pure or mixed stands. Southern biological response equations need to be developed and tested for even-aged and uneven-aged stand conditions to allow the STEMS system to be used for the South.

Distance-Dependent Models

The second type of individual-tree model requires intertree distances as an input. In these models, "individual trees" on a plot are assigned certain initial size and spatial distributions. The trees are "grown" according to some function of their size, site, and competitive status. Sometimes a random adjustment is made for microsite and/or genetic variability (e.g., Daniels and Burkhardt 1975). Competitive status for each tree is quantified in terms of a competition index that is a function of the tree's size and the distance to and size of its neighbors. Mortality is usually a function of competition index, tree size, and/or growth. Yield estimates are made by applying volume equations to the estimated dimensions of the trees (Curtis 1972), as in other individual-tree models and diameter distribution models.

Advantages of individual-tree distance-dependent models over distance-independent forms are that (1) growth estimates are possible for specific individual trees and (2) explicit treatment of location may make it easier to assess the effects of area-specific agents (e.g., diseases). Possible disadvantages of this type of model are that they require (1) intertree distances as an input (not usually inventoried), (2) a meaningful competition index for individual trees, (3) more computing time; also, (4) predictions are often stochastic, and (5) the plots that are simulated are small and perhaps uncharacteristic of the stand.

An example of a single-tree distance-dependent model is the PTAEDA model developed by Daniels and Burkhardt (1975). The PTAEDA model simulates the growth of loblolly pine under a wide range of management alternatives. The two major subsystems in PTAEDA deal with the generation of an initial precompetitive stand and the growth and dynamics of that stand. After PTAEDA was developed for old-field stands, subroutines were added to simulate the effects of site preparation, fertilization, and thinning on tree and stand development (Daniels and Burkhardt 1975). Trees are "grown" annually according to their size, site quality, and intertree competition. The probability of survival for each tree is calculated from a function relating each tree's individual vigor and its competitive stress as measured by estimates of photosynthetic potential. Growth is adjusted stochastically to simulate genetic and microsite variability. Survival probability is used to stochastically determine annual mortality.

Effects of certain management practices are incorporated into PTAEDA by modifying the original growth function through subroutines to simulate the effects of site preparation, thinning, and fertilization on tree and stand development (Daniels and Burkhardt 1975). The efficiency of site-preparation is expressed as the degree to which a cutover site approaches old-field conditions. Growth reductions on cutover land are assumed to be due solely to competing vegetation, because degradation in site quality caused by past management practices could be described by initially specifying a lower site index (Daniels and Burkhardt 1975). Similarly, the response to fertilizer treatments could be described as an increase in site quality, as suggested by Ek and Monserud (1974) and Hegyi (1974). For this reason, a site adjustment factor that acts as a multiplier for site index for fertilized stands is built into the model.

An individual-tree model has also been developed for seeded loblolly pine (Daniels et al. 1979a). However, the growth and mortality components had been developed for plantations. Initial results indicate a need to calibrate these relationships for seeded stands (Daniels et al. 1979a). In regard to computing time requirements for single-tree distance-dependent models, Daniels et al. (1979b) found execution time per stand estimate for the PTAEDA model was 55 times that of the diameter distribution model constructed by Burkhardt and Strub (1974) and 1,378 times that of the whole stand model developed by Burkhardt et al. (1972b).

GROWTH AND YIELD INFORMATION BY FRES ECOSYSTEM AND TIMBER TREATMENT CLASSES

The majority of the different classes of models discussed above provide growth and yield information that applies to even-aged forest types. More specifically, most of the models are for plantations and natural stands in the loblolly-shortleaf and longleaf-slash pine FRES ecosystems.

Other models pertain to thinned upland oak-hickory (Dale 1972), unthinned bottomland hardwoods (Smith et al. 1975, Gardner et al. 1982), and thinned and unthinned yellow-poplar (Schlaegel and Kulow 1969, Beck and Della-Bianca 1970, 1972, 1975). The models by Smith et al. and Gardner et al. can be used for the oak-gum-cypress FRES ecosystem, while Dale's work can be applied to the oak-hickory FRES ecosystem. Because yellow-poplar is commonly present in the oak-hickory type, the models for this species may also be useful in modeling this ecosystem's timber production.

Hepp (1981) incorporated most available growth and yield information by forest type into eleven simulator subroutines in a FORTRAN computer program called YIELD. The user enters stand conditions and financial data and can obtain stand-level growth, yield, and financial analyses. The eleven simulators model seven even-aged forest types: loblolly pine, longleaf pine, shortleaf pine, slash pine, eastern white pine, yellow-poplar, and upland oak. Yield estimates for thinned and unthinned

stands of the southern pines, yellow-poplar, and upland oak are possible. A modification of the program was designed to meet information needs for implementation of linear programming models in National Forest System (NFS) Region 8.

A program similar in concept to YIELD has been developed for loblolly pine by Myers (1977a). The program, YLDTBL, uses available loblolly pine growth and yield information to predict value and yield of planted stands, over the site range of the species, under various management alternatives. Timing and severity of thinnings, length of rotation, and type of harvest can be modified to compare the effects of various management strategies on timber yield. The program can be modified for use with other species, provided that the necessary growth and yield information is available (Myers 1977a). A modified version of YLDTBL that provides yield estimates of both loblolly pine and deer forage has also been published (Myers 1977b). Input variables include stand prescriptions, controls on management, stumpage prices, and costs of various activities and practices. The program is applicable to loblolly pine plantations in east Texas and Louisiana, but (subject to the same information needs as YLDTBL) can be readily modified for other species or areas (Myers 1977b).

GENERAL COMPARISONS OF TIMBER PRODUCTION MODELS

Timber inventory projection models applied in the South have been developed following direct and indirect strategies. Direct methods, such as TRAS, have been used in most large-scale timber supply analyses. Generalized stand table projection models use conventional timber inventory data and are relatively simple and inexpensive to use, but they need a large data base, cannot easily model different forest management schemes, are conceptually difficult to interpret, and reliable tree size and distribution information for smaller areas is hard to extract. Recent research to improve southern pine growth and yield modeling for large geographical areas includes techniques based on age-class representation of the timber inventory.

Indirect methods have been more widely applied. Whole stand models predict stand-level volumes from stand-level characteristics and comprise most of the timber production models located in the literature. Compatible whole stand models allow future timber volume to be derived via mathematical integration of timber growth with respect to time. Age, site, and density are used in predicting stand volumes in whole stand models. Diameter distribution models use Beta, Weibull, and Johnson S_{BBB} probability density functions to represent the distribution of the tree diameters within age site, and density classes. These models can provide volume information by size or diameter classes or aggregations of diameter classes. Individual-tree models simulate stand development using the individual tree as the basic growth unit. The only species in the South that has been

modeled on an individual-tree basis is loblolly pine (Daniels and Burkhart 1975).

Timber production models for other than pure pine types are not numerous. Management regimes that contain one or several thinnings can be simulated at the stand level for specific stand conditions, but the simulation of timber management at more aggregate levels is not well developed. Quantitative guidelines are also not well developed for estimating the progression of understocked and overstocked stands.

Although uneven-aged management of southern pine under the selection system may be an attractive management alternative for many nonindustrial forestland owners, few timber production models are available for uneven-aged stands (Murphy and Farrar 1982, 1983; Farrar et al. 1984). Most uneven-aged modeling has been for mixed hardwood species. The predictor variables most frequently used in models for uneven-aged stands are density (basal area or numbers of trees) and elapsed time. A generally accepted site quality measure has not been established for uneven-aged stands but even-aged site index (estimated from suitable trees) or soil-site index have interim utility.

COST INFORMATION

Information on the cost of providing timber under various forestland management alternatives is required for an economic analysis of timber production. As Samuelson (1976) states, costs and productivity returns are merely opposite sides of the same relationship. The total cost of producing any level of timber output consists of both variable and fixed components. The magnitude of the fixed cost component does not vary with the level of output. A cost function consists of an explicit function of the level of timber management inputs multiplied by the variable cost per unit of input, plus the cost of the fixed inputs.

Forest management costs involve complex, interdependent interactions among the factors of production—capital, labor, land, and other materials. The variety of input combinations used to produce timber is controlled by their marginal rate of technical substitution and relative costs of the inputs. Factors of production can be substituted for each other over a finite output range, although the relatively long period of production allows for many possible adjustments for intertemporally linked investments on a particular ownership.

Three basic alternative methods for estimating the total costs of producing different levels of outputs in economic analyses are: (1) classification of costs for a process into fixed, variable, and semivariable components using an accounting framework, on the basis of inspection and judgment; (2) estimation of the relationships of cost to output on the basis of engineering conjectures and past cost behavior; and (3) determination of the functional relationship of cost to rate of output by statistical analysis of recorded cost, output, and other operating conditions (Dean 1966). These approaches need not be mutually exclusive. Often two or more of

them are used together, as shown in the following summary of reported cost information across RPA timber treatment classes (A = accounting/survey, S = statistical or econometric estimates, D = Delphi estimates):

Management practice	Type of information
A. Regeneration	
1. Site preparation	
a. Mechanical for planting	A, S
b. Seedbed preparation	A, S
2. Artificial	
a. Machine planting	A, S
b. Hand planting	A, S
c. Seeding	S
3. Stand or type conversion	A, D
B. Density control	
1. Chemical removal	A, S
2. Prescribed burning	A, S
3. Release cutting	A
4. Thinning	
a. Precommercial	A
b. Commercial (harvesting costs)	A
C. Other	
1. Fire protection	D
2. Insect and disease protection	—

ACCOUNTING/SURVEY APPROACH

The accounting/survey approach involves classification of timber management costs based on inspection and surveys. One problem is that fixed, variable, and semivariable costs have usually not been separated out for the timber management practices; other problems also exist. Economies of scale have not been accounted for in most forestry cost surveys (e.g., unit cost declines with more acres treated), although unit costs by different acreage or volume classes could be estimated (Row 1978, Cubbage 1983). Categories of management practices used over the years have also varied, as has the embodied technology, which hampers trend analysis. Fluctuations in such factors as wage rates and material prices can usually be corrected for by utilizing a price or cost index to convert estimates to constant dollars.

Cost averages for forestry practices have been calculated from a series of surveys of individuals, public agencies, and private firms in the South over the period 1952–1979 (Moak 1982). These surveys were initiated by Worrell (1953); they are listed in appendix 4. The surveys provide average cost estimates for the following treatments: prescribed burning; mechanical site preparation; planting by hand and machine; chemical removal of undesirable trees; timber cruising; harvest marking; mechanical seedbed preparation in established stands; and cutting to release young growth. The southern states are stratified into three regions: the Southern Coastal Plain, which includes the area south of

the Savannah River and below the fall line in Georgia westward along the Gulf Coast; the Northern Coastal Plain, which includes the area north of the Savannah River and east of the fall line; and the Piedmont, which includes the region in the Southeast between the fall line and the mountains plus the upland areas from Alabama westward through Arkansas.

The costs are further classified according to site characteristics (more difficult than average, average, less difficult than average) and cost components (direct labor, supervision, equipment, overhead). Moak (1982) analyzed the trends in costs of forest practices in the South and compared them with various price trends, and concluded that costs have increased relatively sharply over the past three decades.

Sunda and Lowry (1975) also used a survey technique to develop cost estimates for three different types of loblolly pine regeneration practices: seed-tree, shelterwood, and planting. Twenty land management companies, agencies, or consultants were asked to supply cost information on loblolly pine regeneration procedures performed in 1973 and 1974. The area examined in this study is east Texas, Louisiana, and Arkansas. Cost estimates were similar to those reported for the Southern Coastal Plain by Moak and Kucera (1975).

For each of the three methods, three cases were considered: exceptionally favorable conditions; average conditions; more difficult conditions—especially with regard to hardwood competition. All cases were analyzed for an even-aged stand of loblolly pine harvested at age 40. The elements of regeneration cost considered were: mechanical site preparation (four possible methods); chemical hardwood control; precommercial thinning; marking trees for seed sources; prescribed burning; and planting by hand or machine. The regeneration method and case being analyzed determine which particular cost elements contribute to the total cost of each regeneration scenario (Sunda and Lowry 1975).

The accounting approach provides no way to correct timber cost data explicitly for changes in technology or other conditions that influence cost behavior. These conditions must remain constant for accurate results to be obtained.

ENGINEERING/DELPHI APPROACH

Experience with technical requirements of timber production, including observation of past input requirements and cost behavior, can be used to make systematic conjectures about cost behavior for prospective management practices. The engineering method relies upon expert knowledge and pooled judgments of practical operators (Dean 1966). It also has been characterized as the “synthetic” method—building up descriptions of cost functions from detailed study of components in a production process and integrating those components to represent the total production process.

The Delphi approach has probably been more widely used in natural resource management, where a team of

experts evaluates historical cost behavior to improve their judgments. Two typical features of the Delphi technique are:

1. There is more than one round of questioning—that is, the experts are asked for their opinions on each question more than one time.

2. Controlled feedback is provided. Respondents are told about the group's responses on the preceding round. On later rounds, respondents with extreme answers are asked to provide reasons, and these reasons are summarized anonymously for the next round.

The engineering and Delphi methods are similar. Both rely on experience and judgment, although to varying degrees. Engineering cost estimates are typically constructed in physical units. The man-hours required are converted into dollars at current or prospective prices. The engineering method may be replaced by the Delphi method when experience and records do not provide an adequate historical basis for measuring cost behavior. Engineering and Delphi estimates also supplement statistical or accounting analyses when it is necessary to project cost behavior beyond the range of past timber management experience, or to estimate the effects of major technological or scale changes upon cost behavior.

Information requirements of regional or national timber supply assessments often require that regional forestry experts be convened and asked to provide estimates of costs and other information elements that are not available from other sources. In some cases this is to fill information gaps; in others it may extend to almost complete development of needed data bases. Two examples of this procedure in forestry are the regional timber investment panels utilized in the USDA Forest Service (1981a, 1981b) study, and the multiresource production experts for the Ashton et al. (1980) study.

There is a vast literature on the Delphi technique, but comparatively little empirical work is available on the advantages of several key aspects of the Delphi techniques (e.g., iterative procedure and feedback) over the typical mail survey. Armstrong (1978) is critical of the attention that the Delphi technique has received in forecasting. Sackman (1974) states that the accuracy of this technique is necessarily suspect so long as Delphi questions are not empirically linked to objective and independently verifiable criteria. Sackman concludes that the technique is essentially unreliable and scientifically unvalidated. However, these liabilities are counterbalanced somewhat by the immediate need to apply this technique in some natural resource supply analyses where the notion of expert opinion, low cost, convenience, and simplicity of the method make it attractive.

STATISTICAL APPROACH

The statistical approach uses multiple regression or other statistical techniques to estimate a functional relationship between cost and timber output. Hence, the statistical method can accommodate more variation in underlying conditions than the accounting approach

because variations can be accounted for by using explanatory variables.

Statistical analysis of timber production cost behavior can use either cross-sectional data (simultaneous observation of costs of different, but similar, timber treatment areas) or time series data (sequential observation of costs for identical treatment opportunities over a period of time). Cross-sectional observations are more common in forestry than time series data, which require many years to accumulate. The difference between cross-section and time series data is somewhat analogous to temporary plots versus remeasurements.

A difficulty with using cross-sectional data is that it is not easy to locate enough treatment areas for an adequate sample. The areas need to be sufficiently similar in resource condition, management methods, and records. They must also differ in size to analyze economies of scale. For the use of time series data, it is not likely that technology, management methods, and other conditions have remained essentially constant over the time required to collect a sufficient number of time series data points. In some cases, cross-sectional and time series data can be pooled to help circumvent such problems (Judge et al. 1982).

Econometric techniques, which use economic theory, mathematical economics, and statistical inference as an analytical foundation for quantifying relationships among economic variables, have been used to estimate costs of timber production. Statistical or econometric estimation is generally based on nonexperimental cost data, where observations of a system are not subject to experimental control. This contrasts with the data in growth and yield studies based on experimental designs. Further, cost studies have usually been conducted independently of the growth and yield studies discussed earlier. Consequently, geographical bases, definitions, etc., may differ markedly between these sets of studies, making comparison and cross-reference difficult.

Nationwide studies by Row (1971) and Mills et al. (1984), based on Forest Service contract data, present cost averages and predictive equations. Row used contracts from FY 1970, stratified according to management practice, method of application, and forest type. Mills et al. used contracts from FY 1975 through FY 1978, stratified according to management practice and forest type. Forest types used to classify the contracts in both studies are Forest Survey types, which are essentially equivalent to the FRES types discussed earlier. Both Row and Mills et al. found it necessary to aggregate several FRES types to obtain sufficient sample sizes. Row found it necessary to aggregate all eastern FRES types to obtain sufficient sample size to develop a regression relationship, including contracts in the Northeast and the Southeast.

Row used 850 of the 1019 contracts awarded in FY 1970. Only combinations of management practice, method, and forest type represented by more than 10 contracts were analyzed. Some of the management practices (e.g., site preparation) could be performed by any of several methods. The equations developed are for: (1) complete site preparation using a bulldozer with blade; and (2) site preparation using a bulldozer with

rake. The equations predict total cost (including Forest Service equipment, labor, materials, and direct administrative cost) and are based on 12 and 15 observations, respectively.

The econometric model developed by Row predicts total cost for each contract as the sum of a fixed cost per contract and a variable cost per acre times the number of acres in the contract. The variable cost per acre is a function of a basic variable cost for each practice-method-forest type combination, acres per tract in the contract, relative accessibility of the tract, and difficulty of the terrain (in terms of obstacles). Each observation was weighted according to its size in acres because the variability in cost was higher for smaller contracts. Weighting in this manner compensates for heteroscedasticity among the observations, permitting a valid regression relation to be developed (Row 1971).

Mills et al. (1984) stratified Forest Service contracts from FY 1975 through FY 1978 according to forest type and management practice. The four practices analyzed are: (1) site preparation for seeding, planting, or natural regeneration, consisting of burning, low intensity preparation, or high intensity preparation; (2) reforestation by hand or machine planting or seeding; (3) intermediate treatment, including precommercial thinning, timber stand improvement, individual or area tree release by aircraft, hand, or machine; and (4) slash disposal.

Aggregate forest types used by Mills et al. (1984) are southern pine and central hardwoods. Equations developed for these aggregate forest types predict direct cost (defined as contract cost plus the cost of Forest Service materials used in the contract) for the following forestry practices: site preparation for southern pine; reforestation for southern pine; intermediate treatment for southern pine; and site preparation for central hardwoods. These equations were based on 126, 74, 28, and 68 cases, respectively.

Equations developed by Mills et al. (1984) are based only on variables currently known or easily estimated. To select the variables used, a statistical screening procedure is used to determine which variables are most significant. From these, an all-possible value covariance matrix is calculated, and variables with simple correlations of 0.80 or greater are identified. One of the two correlated variables is excluded from further analysis in that stratum. From the covariance matrix, a set of all possible regression equations is developed. The regression in this set that has the least unexplained variability (as measured by Mallows's C_p statistic) is withdrawn for further analysis.

Variables present in this regression are noted, and observations complete in these variables are used to calculate a second all-possible value covariance matrix. From this second matrix, a second set of all-possible regression equations is calculated. The regression equation in this second set of equations that has the least unexplained variability is used as the final equation (Mills et al. 1984).

Vasievich (1980) also used Forest Service information to develop an econometric relationship to predict the cost of hazard reduction burning. He analyzed 408 hazard reduction burn plans from Coastal Plain national

forests extending from South Carolina to Texas. The burns were all successfully completed from 1972 to 1975. Equations were developed to predict man-days of labor, chains of plow line, and chains of fireline. The dependent variables are the size of the burn area (acres) and the age of the rough (i.e., years since last burn). Overhead, direct, and indirect costs were derived from these equations using assumptions and supplemental information provided in the paper.

Overhead costs cover fixed expenses that are necessary for a burning program but that cannot be related to a specific burn. These costs are assumed to be a fixed percentage of all direct and indirect costs. Indirect costs are for such items as planning and transportation of labor and equipment. Direct costs are outlays for labor, materials, and equipment to plow firelines before the burn, to do the burning itself, and to mop up afterward. Costs are expressed in 1976 dollars and compare closely with the Moak et al. (1977) cost estimates. The Vasievich (1980) costs are slightly lower, possibly because average burn size is larger or because only successfully completed burns are considered (Vasievich 1980).

INTEGRATION OF TIMBER PRODUCTION AND COST INFORMATION

Cost studies of timberland management practices have usually been conducted independently of growth and yield studies. However, several studies have combined cost information with growth and yield information, usually for the financial analysis of timber management decisions at the stand level in the South. Review of these studies can help identify the "weak links" for these integrated analyses, in the context of the (relative) value of possibly obtaining additional information for different study components.

One of the more comprehensive models that integrates a broad range of timber growth/yield and cost information for southern ecosystems is the Georgia Supply (GASPLY) model (Montgomery et al. 1976, Robinson et al. 1978). GASPLY, which is based on a FORTRAN computer program, estimates the long-run timber supply from even-aged forests in Georgia. The GASPLY model aggregates USDA Forest Service survey plots into acreage cells, each homogeneous with respect to region, subregion, forest type, owner, site quality, and physiographic class. Three management plans are analyzed—custodial, natural stand, and plantation. The custodial plan implies no management and minimal costs; property taxes are the only cost outlay. The specific elements of the cost of the natural stand and plantation plans reflect currently accepted methods of regeneration and management. Costs and benefits included in each plan are compared on a perpetual rotation basis; maximum present net worth is the criterion used to assign a plan to a cell.

The user of GASPLY specifies a long-run demand equation, and GASPLY will develop a management prescription that will meet long-run quantity demanded. Because maximum present net worth is the criterion used to select optimal management plans, the GASPLY

prescription is economically efficient (Robinson et al. 1978). Robinson et al. (1981) used GASPLY to develop an economic growth goal for the Southeast. The area covered in this study (Florida, Georgia, North Carolina, South Carolina, and Virginia) is stratified into three physiographic areas: the Coastal Plain, the Piedmont, and the mountains. Five forest types were defined: longleaf-slash pine, loblolly-shortleaf pine, oak-pine, upland hardwoods, and bottomland hardwoods. Yield equations for natural stands and plantations of loblolly and slash pines were adapted from Coile and Schumacher (1964) and Schumacher and Coile (1960). Yields for hardwood stands were developed from Knight's (1978) analysis of USDA Forest Service survey plots in North Carolina and Virginia. Stumpage prices were developed from Timber Mart-South price reports (Norris 1976); cost estimates were obtained from a survey of industrial timberland managers, National Forest managers, and State Foresters' staffs (Robinson et al. 1981).

In another regional study, the USDA Forest Service (1981a, 1981b) describes economic opportunities to increase softwood production on private lands. This study used the TRAS model discussed earlier and the Timber Assessment Market Model (TAMM) (Adams and Haynes 1980) to project long-run timber supply, and summarized the results of TAMM projections for four levels of investment. These investment levels are comprised of different intensities and schedules of the timber treatment classes described in Table 2. Two of the investment levels give special attention to private lands; they include immediate investments in softwood management on private lands beyond those expected to occur under continuation of present management. The array of investments are presented that would return 4% and 10% real rates of return.

Costs given are the total present value of the cost (per cubic foot and per acre) for the investment (Table 2) plus the discounted value of any follow-up costs associated with each treatment. Treatment costs given for the Southeast region are: (1) control, including precommercial thinning, prescribed burning, stand cleaning, release from competition, and commercial thinning; (2) stand conversion, which reflects a decision to harvest or clear low-value or low-growth hardwoods and replace them with pine; (3) regenerating nonstocked land (defined as less than 16.7% stocked with growing stock trees) including site preparation and planting; (4) regenerating hardwoods, consisting of harvesting bottomland hardwoods and preparing the site for natural regeneration; and (5) harvest and regeneration of the existing stand. Costs presented for the Midsouth region are: (1) stocking control; (2) regenerating nonstocked acres; and (3) harvest and regeneration of the existing stand (USDA Forest Service 1981b).

Timber investment analyses at the stand level include that by Anderson and Gutterberg (1971) for the conversion of mixed oak-pine stands to stands of pure pine. They constructed investment guides by using growth and yield information reported by Bennett and Clutter (1968) and Lenhart (1968) for slash and loblolly pine. An average conversion cost of \$40 per acre was used.

Anderson (1972) used these yield models to derive economically oriented production functions. The functions are developed from size-class data. Per-acre volumes and cumulative number of trees in percent are given for 20-, 25-, and 30-year production periods on medium and good sites. Such yield information is useful in determining economically efficient rotation length.

Weaver and Osterhaus (1976) derived investment schedules for planted loblolly pine from regeneration costs and regeneration scenarios developed by Sunda and Lowry (1975). Loblolly pine yields and prices were adapted from Anderson and Guttenberg (1971) and Dierauf and Marler (1965). Using this information, Weaver and Osterhaus calculated the net present value of the regeneration cases discussed by Sunda and Lowry for low, medium, and high quality site classes.

Hardie (1977) used dynamic programming to determine an optimal thinning strategy and rotation length for planted loblolly pine in the mid-Atlantic region. Yield estimates are from a model developed at Virginia Polytechnic Institute and State University. Several economic parameters are varied in Hardie's model. Among these are stumpage price trends, discount factors, costs of plantation establishment, property taxes and other annual charges, sporadic or periodic costs incurred during the rotation, land rent, and trends in costs. Maximum present net worth is the criterion used to select the optimal management plan.

The degree of uncertainty inherent in estimating future components of timber supply in the studies above is strongly related to the aggregation schemes employed, which by their nature condense diverse and complex relationships into a relatively small number of essential characteristics. The broad geographical range of most aggregate analyses that integrate timber production and cost information invariably includes diverse timber resource conditions and potentials. Further, aggregation and uncertainty in timber supply modeling are related in part to the quantity and quality of historical data available as a basis for projection. Although the levels of timber growth and yield data have been augmented substantially during the last several decades, substantial data deficiencies remain for both biological and economic dimensions of timber supply modeling.

OVERVIEW AND CONCLUSIONS

Information for estimating the input and output relationships for southern timber production is largely based on experiments that selected very homogeneous timber stand situations. In contrast, timber yield information for more typical or "woods-run" heterogeneous stands is relatively limited. Although the growth and yield studies have advanced well beyond examination of fully stocked stands, a parallel positive bias presently exists because of selection of uniform plots in managed yield studies. Southern growth and yield information accumulation has accelerated, but some important relationships among timber production inputs and outputs still require further study. For example, long-term studies are necessary to determine the treatment

response of stands in terms of diameter distributions and volume of sawtimber, veneer, and poles. Timber production models are only available for a few specified timber management practices for the wide array of stand ages, site qualities, and density levels. The available information is primarily for even-aged pine management, and in particular planted loblolly and slash pine. There are fewer managed yield tables than those for unthinned stands. Geographical applicability of models is sometimes not well specified, and validation techniques have not been widely discussed in the literature.

There is more timber growth and yield information available for even-aged stands than for uneven-aged ones. Research for uneven-aged timber management yields has expanded in recent years (Farrar et al. 1984). Interest in uneven-aged timber management as a practical alternative is increasing, particularly for private nonindustrial ownerships in the South (Murphy 1980). These ownerships comprise approximately three-quarters of the timberland in the region.

Although efforts continue to improve information on the development of stands under specified timber management regimes, additional timber production and cost information is also needed for passive or "no management." Because many stands are not managed actively, the natural transitions among forest types and composition of stands after harvest is an important consideration in long-term timber supply modeling.⁵ Studies by Boyce and Knight (1979, 1980) indicate many nonindustrial, private forest owners passively permit the (biologically) better adapted hardwoods to increase naturally after the harvest of pines. Improved fire protection and shifting agriculture have also contributed to changes in the region's distribution of forest types.

Productivity resulting from inputs into timber production can be analyzed using production functions that depict the transformation of inputs into timber output. Technology in timber production consists of a collection of techniques (both available and implemented ones), with each technique represented by a production function. A change in the collection of techniques constitutes technological change, such as implementation of regeneration methods involving genetically improved stock. More intensive timber production methods have been applied in the South, but empirical analysis of related aggregate trends has been limited.

The stochastic nature of timber growth and yield estimates, related to the substantial uncertainty associated with long-term timber production processes, has not been widely discussed in the literature. Deterministic models of growth and yield are often reported without reflecting stochastic tendencies of long-range growth and yield estimates. Impacts on growth and yield from climatic vagaries, fire, insect, or disease epidemics are difficult to predict and depend in part on management and utilization trends. Southern pine beetle effects in the South are being analyzed in a large research ef-

⁵Alig, Ralph J., James G. Wyant, and Herbert A. Knight. 1983. *Analysis of forest type transition in the Southeast*. 33 p. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

fort, and Reed et al. (1980) have made long-term projections of beetle damage using the TRAS model. Past regional studies, such as USDA Forest Service timber assessments, usually project mortality based on historical patterns.

Much less data has been collected and research conducted on the costs for various forestland management alternatives than for timber growth and yield production. The main source of time series data on costs of forestry practices is a series of related accounting surveys over the period 1952–1979 (Moak 1982). Statistical analyses of timber production cost relationships, based on regression or econometric equations, are the other major source of timber management cost information. These studies are usually based on cost information from Forest Service contracts. Replication or expansion of these types of analyses has been quite limited. Delphi techniques have been used to provide cost estimates in cases where it is not possible to obtain needed information from statistical analyses or surveys.

Past integration of timber production and cost information has been primarily for stand-level analyses. One of the few regional models for the South that combines aspects of timber production and management costs is the GASPLY model. This model can accommodate empirical growth and yield data collected in the major statewide forest resource inventory efforts.

Aggregation of growth and yield and cost information in the analysis of regional timber supply warrants more scrutiny in future studies. Trade-offs need to be examined between two kinds of costs: (1) those derived using variables that are numerous and/or difficult to obtain or estimate, and (2) the costs associated with the unsatisfactory predictions that may result if the number of variables is small, thus sacrificing detailed information.

Aggregation procedures are judged satisfactory by Green (1964) when the cost of more detailed information outweighs the greater reliability of the results that could be obtained by using more detailed information. That judgment depends in part on the purpose of the investigator in conducting regional timber supply studies. Gauging the associated “reliability” of results in long-range timber supply analyses is not likely to be straightforward and may be somewhat subjective in nature.

Green's evaluation of aggregation procedures is related to the concept of “consistent” aggregation, where the use of information more detailed than that contained in the aggregate would make no difference in the results of the analysis. In addition to these theoretical aggregation problems, the integration of timber growth and yield and economic information in timber supply studies is influenced by institutional considerations (e.g., political or administrative groupings) and further complicated by differences in emphasis among disciplines.

In summary, major information needs related to analyses of timber supply in the South include modeling of growth and yield for uneven-aged forest management and the mixed oak-pine FRES types, and costs for implementing most forestland management alternatives. Much more attention has been devoted to the biological and mensurational dimensions of southern timber

supply in past data collection and research efforts than to the cost aspects. Differences in underlying study conditions, definitions, and other characteristics create some problems in combining the cost information that has been accumulated with that from growth and yield studies. Significant strides have taken place over the last several decades in addressing such problems, and further improvements in timber supply analysis will depend in part on measures taken to strengthen existing data sources.

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APPENDIX 1

SUMMARY OF TIMBER GROWTH AND YIELD MODELS SURVEYED¹

Table A1.—Summary of models surveyed

Author	Year	Principal species
WHOLE STAND MODELS		
Plantations		
Bennett et al.	1959	Slash pine
Burkhart et al.	1972b	Loblolly pine
Burkhart and Sprinz	1984	Loblolly pine
Coile and Schumacher	1964	Loblolly, slash pines
Goebel and Warner	1969	Loblolly pine
Lohrey	1979	Longleaf pine
Sullivan and Williston	1977	Loblolly pine
Natural Stands		
Beck and Della-Bianca	1972, 1975	Yellow-poplar
Bennett	1970, 1980	Slash pine
Brender and Clutter	1970	Loblolly pine
Burkhart et al.	1972a	Loblolly pine
Dale	1972	Upland oak-hickory
Farrar et al.	1984	Loblolly, shortleaf pines
Gardner et al.	1982	Hardwoods
Murphy	1982	Shortleaf pine
Murphy	1983	Loblolly pine
Murphy and Beltz	1981	Shortleaf pine
Murphy and Farrar	1982, 1983	Loblolly, shortleaf pines
Murphy and Sternitzke	1979	Loblolly pine
Schlaegel and Kulow	1969	Yellow-poplar
Schlaegel et al.	1969	Yellow-poplar
Schumacher and Coile	1960	Southern pines
Smith et al.	1975	Hardwoods
Sullivan and Clutter	1972	Loblolly pine
DIAMETER DISTRIBUTION MODELS		
Plantations		
Burkhart and Strub	1974	Loblolly pine
Cao et al.	1982	Loblolly pine
Clutter and Belcher	1978	Slash pine
Clutter and Jones	1980	Slash pine
Dell et al.	1979	Slash pine
Feduccia et al.	1979	Loblolly pine
Lenhart	1972	Loblolly pine
Lenhart and Clutter	1971	Loblolly pine
Lohrey and Bailey	1977	Longleaf pine
Matney and Sullivan	1982	Loblolly pine
Smalley and Bailey	1974a	Loblolly pine
Smalley and Bailey	1974b	Shortleaf pine
Smith	1978	Loblolly pine
Natural Stands		
Beck and Della-Bianca	1970	Yellow-poplar
Schreuder et al.	1979	Slash pine
INDIVIDUAL-TREE MODEL		
Plantations		
Daniels and Burkhart	1975	Loblolly pine

¹Based on tables provided by Dr. Harold Burkhart, Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

APPENDIX 2

SELECTED CHARACTERISTICS AND NATURE OF DATA USED IN TIMBER GROWTH AND YIELD MODELS

These tables are based on tables 1 and 2 of a report by Burkhart et al. (1981); several additions incorporate information on more recent studies.

Table A2.—Old-field and other plantation models

Model	Geographic location	Stand treatments	Number of observations	Plot size	Range of data		
					Age	Site index 25	Density
				<i>acres</i>	<i>years</i>	<i>feet</i>	<i>trees/acre</i>
OLD-FIELD PLANTATION MODELS							
Loblolly pine							
Burkhart and Strub (1974)	Piedmont and Coastal Plain in Virginia; Coastal Plain in Delaware, Maryland, and North Carolina	Unthinned	186	0.1	10-35	47-84	300-2900
Burkhart et al. (1972b)	Piedmont and Coastal Plain in Virginia; Coastal Plain in Delaware, Maryland, and North Carolina	Unthinned	189	0.1	9-35	47-84	300-2900
Burkhart and Sprinz (1984)	Piedmont and Coastal Plain in Virginia	Thinned	103	0.3	10-40	50-70	--
Cao et al. (1982)	Piedmont and Coastal Plain in Virginia	Thinned	128	0.2	12-30	50-70	355-1305
Goebel and Warner (1969)	Piedmont in South Carolina	Unthinned	200	64	10-25	40-75	500-1400
Lenhart (1972)	Interior West Gulf	Unthinned	219	65	10-30	40-70	500-1200
Lenhart and Clutter (1971)	Georgia Piedmont	Unthinned	226	64	9-33	40-80	750-1650
Matney and Sullivan (1982)	South	Thinned	--	--	--	--	--
Smalley and Bailey (1974a)	Highland in Tennessee, Alabama, and Georgia	Unthinned	267	0.05	10-31	31-89	202-2240
Slash pine							
Bennett and Clutter (1968)	Coastal Plains in Georgia and north Florida	Unthinned	478	--	15-30	50-80	--
Bennett et al. (1959)	Georgia middle Coastal Plain, Carolina sandhills	Unthinned	308	Varied	10-28	30-80	110-5400
Clutter and Jones (1980)	Georgia, Florida, Alabama, and Mississippi	Thinned	212	0.25	9-32	47-80	(Basal area 25-150 ft ² /acre)
Shortleaf pine							
Smalley and Bailey (1974b)	Highlands in Tennessee, Georgia, and Alabama	Unthinned	104	Varied, usually 0.05	11-35	26-58	400-4500
NON-OLD-FIELD PLANTATION MODELS							
Loblolly pine							
Feduccia et al. (1979)	East Texas, Louisiana, southern Arkansas, and southern Mississippi	Unthinned	409	Varied but >0.1	3-45	22-78	250-1500
Smith (1978)	Lower Coastal Plains in Carolinas, Georgia, and north Florida	Unthinned	226	Varied	10-30	20-70	300-900
Sullivan and Williston (1977)	Loessial soils in Arkansas, Mississippi, and Tennessee	Thinned	499	Varied	6-30	60-110	(Basal area 1-139 ft ² /acre)

NON-OLD-FIELD PLANTATION MODELS—(Continued)

Table A2.—Old-field and other plantation models—(Continued)

Model	Geographic location	Stand treatments	Number of observations	Plot size	Range of data		
					Age	Site index 25	Density
				<i>acres</i>	<i>years</i>	<i>feet</i>	<i>trees/acre</i>
Slash pine							
Clutter and Belcher (1978)	Coastal Plain in Georgia and Florida	Unthinned	487	Varied	--	--	--
Dell et al. (1979)	West Gulf: east Texas, Louisiana, and Mississippi	Same as Feduccia et al. (1979)	399	--	3-32	23-87	250-2500
Longleaf pine							
Lohrey (1979)	South Louisiana, and east Texas	Thinned Unthinned	457	Varied	16-42	33-68	(basal area 40-190 ft ² /acre)
Lohrey and Bailey (1977)	Central Louisiana, and east Texas	Unthinned	260	Varied, 0.10-1.25	16-38	29-73	250-2500
BOTH OLD-FIELD (*) AND NON-OLD-FIELD (**) PLANTATION MODELS							
Loblolly pine							
Coile and Schumacher (1964)	South	Half of the plots were thinned one or more times	370* 28**	0.10 (6-10 yr) 0.20 (> 10 yr)	5-35	35-80	--
Daniels and Burkhart (1975)	Piedmont and Coastal Plain in Virginia; Coastal Plain in Delaware, Maryland, and North Carolina	Unthinned	189* 51**		8-35	47-84	300-2900
Slash pine							
Coile and Schumacher (1964)	South	Half of the plots were thinned one or more times	370* 28**	0.10 (6-10 yr) 0.20 (> 10 yr)	5-35	35-80	--

Table A3.—Natural stand models

Model	Geographic location	Stand treatments	Number of observations	Plot size	Range of data		
					Age	Site index 25	Basal area
				<i>acres</i>	<i>years</i>	<i>feet</i>	<i>ft²/acre</i>
Loblolly pine							
Brender and Clutter (1970)	Hitichi Experimental Forest in Georgia Piedmont	Light thinning or improvement cut	179	Varied	15-70	50-100	10-120
Burkhart et al. (1972a)	Coastal Plains in North Carolina and Virginia; Piedmont Virginia	Unthinned	121	0.10	13-77	53-92	35-217
Clutter (1963)	Georgia, Virginia, and South Carolina	Thinned	102	0.25	21-69	53-110	30-154
Murphy (1983)	South Arkansas, Louisiana, and East Texas	Thinned unthinned	296	Variable radius	> 20-51 +	> 70-101 +	> 20-121 +
Murphy and Sternitzke (1979)	West Gulf: east Texas, Louisiana, and Arkansas	Thinned	145	--	12-85	68-127	17-137
Schumacher and Coile (1960)	Coastal Plain from Chesapeake Bay to Mobile Bay	Unthinned	420	0.20	20-80	60-120	96-198
Sullivan and Clutter (1972)	Georgia, Virginia, and South Carolina	All plots were thinned	102	0.25	21-69	53-110	30-154
Uneven-aged loblolly-shortleaf pine							
Farrar et al. (1984), Murphy and Farrar (1982, 1983)	South Arkansas, and north Louisiana	Thinned	310	2.5-40 +	² 1-18	80-90	> 20-100 +
Murphy and Farrar (1982, 1983)	South Arkansas	Thinned	310	2.5-4.0 +	² 1-18	80-90	> 20-100 +
Slash pine							
Bennett (1970)	Tampa, throughout east and west Florida to Cordele and Savanna, Georgia	Thinned	82	0.25	20-60	60-100	50-175
Bennett (1980)	South Georgia, north and west Florida	Unthinned Thinned	176 121	0.25 0.25	20-50	60-100	25-175
Schreuder et al. (1979)	Georgia and Florida	Unthinned	175	0.25	17-68	43-104	³ 22-450
Schumacher and Coile (1960)	Throughout commercial slash pine range	Unthinned	231	0.20	20-30	50-100	³ 133-1308

Table A3.—Natural stand models—(Continued)

Model	Geographic location	Stand treatments	Number of observations	Plot size	Range of data		
					Age	Site index 25	Basal area
				<i>acres</i>	<i>years</i>	<i>feet</i>	<i>ft²/acre</i>
Longleaf pine							
Farrar (1979a)	Northwest Florida, southwest Georgia, south and central Alabama, and south Mississippi	Thinned	¹ 139	0.20	15-80	46-90	8-169
Schumacher and Coile (1960)	Atlantic Coastal Plain	Unthinned	368	0.20	20-80	50-100	³ 165-588
Shortleaf pine							
Murphy and Beltz (1981), Murphy (1982)	West Gulf: east Texas, east Arkansas, Louisiana, and Arkansas	Unthinned	153	--	26-91	44-101	4-94
Schumacher and Coile (1960)	North Carolina, Piedmont	Unthinned	74	0.20	20-80	40-100	93-204
Upland oak-hickory							
Dale (1972)	Kentucky, Ohio, Missouri, Iowa	Thinned	154	Varied, Usually > 0.56/acre	22-90	55-89	--
Yellow-poplar							
Beck and Della-Bianca (1970, 1972, 1975)	Appalachian Mtns. of North Carolina, Virginia, and Georgia	Unthinned (1970), thinned (1972, 1975)	141	0.25	17-76	75-138	44-208 (Prior to thinning)
Schlaegel and Kulow (1969)	West Virginia	Unthinned thinned	123	0.1-0.25	26-80	57-110	60-180
Schlaegel et al. (1969)	West Virginia	Unthinned thinned	123	0.1-0.25	26-80	57-110	60-180
Hardwoods							
Gardner et al. (1982)	South	Unthinned	641	0.20	--	--	--
Smith et al. (1975)	South	Unthinned	641	0.20	--	--	--

¹Number of plots involved.²Elapsed time or cutting cycle length, age is not applicable.³Trees per acre.

APPENDIX 3

INPUTS AND OUTPUTS FOR TIMBER GROWTH AND YIELD MODELS

These tables are based on table 3 from Burkhardt et al. (1981), with several additions pertaining to more recent studies.

Table A4.—Whole stand models for plantations and natural stands

Model	Inputs	Outputs
PLANTATIONS		
Bennett et al. (1959)	Age A Initial spacing Percent survival at age A Site index (base age 25)	Ft ³ volumes (ob and ib) to 2-, 3-, and 4-inch tops ob
Burkhardt et al. (1972b)	Age A Number of surviving trees/acre at age A Site index (base age 25) Site index (base age 25)	Average height of dominants and codominants Ft ³ volumes (ob and ib): total, to 3- and 4-inch tops ob Bd.ft. volumes to 6-inch tops ob
Burkhardt and Sprinz (1984)	Ages A1 and A2 Site index (base age 25) Initial basal area	Ft ³ volumes (ob): total, to 4- and 6-inch tops ib
Coile and Schumacher (1964)	Age A Number of trees/acre planted or surviving Site index (base age 25)	Number of surviving trees/acre Average height of dominants and codominants Basal area and average dbh Total ft ³ volumes ib Feasible to compute ft ³ volumes ob to 4-inch tops ib
Goebel and Warner (1969)	Age A Number of surviving trees/acre at age A Site index (base age 25)	Average height of dominants and codominants Ft ³ volumes ib: total, to 3- and 4-inch tops ob
Lohrey (1979)	Ages A1 and A2 Site Index (base age 25) Initial basal area (B1)	Projected basal area Ft ³ volumes (ob): total Bd.ft. volumes to 8-inch tops ob
Sullivan and Williston (1977)	Ages A1 and A2 Site Index (base age 50) Initial basal area (B1)	Projected basal area Ft ³ volumes (ib): to 3-inch tops ib
NATURAL STANDS		
Beck and Della-Bianca (1972, 1975)	Ages A1 and A2 Basal area at age A1 Site index (base age 50)	Basal area at age A2 Ft ³ volumes, trees 4.5 inches dbh and larger Bd.ft. volumes for trees 11-inches dbh and larger Mean dbh Mean dominant stand height
Beck and Della-Bianca (1975)	(As above) Height of dominant stand	Bd.ft. volumes for trees 11 inches dbh and larger
Bennett (1970, 1980)	Ages A1 and A2 Basal area at age A1 Site index (base age 50)	Ft ³ volumes to 4-inch tops ob, at ages A1 and A2 Bd.ft. volumes of trees 9.6 inches dbh and larger to 8-inch tops (ob) ages A1 and A2 Basal area at age A2
Brender and Clutter (1970)	Ages A1 and A2 Basal area at age A1 Site index (base age 50)	Ft ³ volumes to 4-inch tops at ages A1 and A2 Bd.ft. volumes to 8-inch tops at ages A1 and A2
Clutter (1963)	Ages A1 and A2 Site index (base age 50)	Basal area at age A2 Bd.ft. volumes (ib): total

Table A4.—Whole stand models for plantations and natural stands—(Continued)

Model	Inputs	Outputs
NATURAL STANDS—(Continued)		
Dale (1972)	Age A Basal area at age A Site index (base age 50)	Net annual basal area Growth/acre (2.6-inch dbh and larger) Ft ³ volumes (ob) 2.6-inch dbh and larger Ft ³ volumes (ib) trees 4.6 inches dbh and larger to 4.5-inch tops ob Bd.ft. volumes (ib) trees 8.6 inches dbh and larger to 4.5-inch tops ob
Farrar (1979a)	Ages A1 and A2 Basal area at age A1 Site index (base age 50)	Basal area at age A2 At ages A1 and A2: Total ft ³ volumes (ib and ob) Ft ³ volumes (ib and ob) for trees 3.6-inches dbh and larger to 3-inch tops ob Ft ³ volumes (ib and ob) for trees 9.6 inches dbh and larger to 7-inch tops ob Bd.ft. volumes for trees 9.6 inches dbh and larger to 5-inch tops ib Average diameter
Gardner et al. (1982)	Age A Sapling basal area Pole and sawtimber basal area	Volumes and weights of various stand biomass components
Murphy (1982)	(As above)	(As above) Bd.ft. volumes for trees 9-inches dbh and larger for 4 log rules to 7-inch tops ib
Murphy (1983)	(As above)	Ft ³ volumes for trees 9-inches dbh and larger to 7-inch tops (ob) Bd.ft. volumes for trees 9-inches dbh and larger to 7-inch tops ob at ages A1 and A2
Murphy and Beltz (1981)	Ages A1 and A2 Basal area at age A1 Site index (base age 50)	Basal area at age A2 Ft ³ volumes for trees 5-inches dbh and larger to 4-inch tops (ages A1 and A2)
Murphy and Farrar (1982, 1983)	Elapsed time (cutting cycle) Initial merch. and sawt. basal areas	Projected merchantable and sawtimber basal areas Ft ³ volumes (ib): trees >3.5-inch dbh to 3.5-inch tops (ib) and trees >9.5-inches dbh to 7.5-inch tops ib Bd.ft. volumes for trees >9.5-inches dbh to 7.5-inch tops ib
Murphy and Sternitzke (1979)	(As above)	Basal area at age A2 Ft ³ volumes for trees 5-inches dbh and larger to 4-inch tops ob at ages A1 and A2
Schlaegel and Kulow (1969)	Ages A1 and A2 Site index (base age 50)	Basal area at age A2 Ft ³ volumes (ib): total
Schlaegel et al. (1969)	Basal area at age A1 as above	As above and total ft ³ volumes (ob) Bd.ft. volumes
Schumacher and Coile (1960)	Ages A1 and A2 Basal area at age A1 Site index (base age 50)	Basal area at age A2 At age A1 and age A2: Total ft ³ volumes ib Bd.ft. volumes to 6-inch tops ib. Average heights of dominants and codominants Number of trees/acre
Smith et al. (1975)	Age A State Percent cover by species	Bd.ft. volumes, and ft ³ volumes Total height at age A
Sullivan and Clutter (1972)	Ages A1 and A2 Basal area at age A1 Site index (base age 50)	Basal area at age A2 Total ft ³ volumes ib at ages A1 and A2

Table A5.—Diameter distribution models

Model	Inputs	Outputs
Beck and Della-Bianca (1970)	Age A Site index (base age 50)	For each dbh class: Total ft ³ volumes and to 4-inch tops (ob) Bd.ft. volumes for trees 11-inches dbh and larger to 9-inch tops (ob)
Burkhardt and Strub (1974)	Age A Number of surviving trees/acre at age A Average Height of dominants and codominants	Average height Number of surviving trees/acre Feasible to compute ft ³ volumes (ob and ib): total, to 3- and 4-inch tops ob, using volume equations from Burkhardt et al. (1972b)
Cao et al. (1982)	Age A Site index Total basal area and number of trees per acre	Average height Total ft ³ volumes (ob and ib)
Clutter and Belcher (1978)	Age A1 Average height of dominants Number of surviving trees/acre at age A2	For each dbh class: trees/acre at age A2 Average height Ft ³ volumes to 4-inch tops (ob)
Clutter and Jones (1980)	Age A Site index (base age 50) For each dbh class: Trees/acre Average height Average dbh	Number of trees at age A2 Basal area at age A2 Ft ³ volumes at age A2 Bd.ft. volumes at age A2
Dell et al. (1979)	Age A Trees/acre, planted or surviving Site index (base age 25)	Average height and crown ratio Number of trees/acre Ft ³ volumes (ob and ib): total, and to 2-, 3-, and 4-inch tops (ob)
Feduccia et al. (1979)	Age A Number of trees/acre planted or surviving Site index (base age 25)	Average height and crown ratio Number of surviving trees/acre Ft ³ volumes (ob and ib): total, to 2-, 3-, and 4-inch tops ob
Lenhart (1972)	Age A Number of surviving trees/acre at age A Site index (base age 25)	Average height Number of surviving trees/acre Ft ³ volumes (ob and ib): total, to 2-, 3-, and 4-inch tops ob
Lohrey and Bailey (1977)	Ages A1 and A2 Number trees/acre at A1 Height of dominant stand	Number of trees/acre at A2 Basal area/acre at A2 Ft ³ volumes (ib and ob): total, trees 3.5 inches dbh and larger to 4-inch tops (ob)
Schreuder et al. (1979)	Age A Trees per hectare Site Index (Base age 50)	Tree dbh, height, and volume distributions (2 parameter Weibull) Trees per acre by dbh class Mean tree height by dbh class Total volumes (ob) per hectare in m ³ and cords by dbh class and stand
Smalley and Bailey (1974a,b)	Age A Number of trees/acre planted or surviving Site index (base age 25)	Average height Number of surviving trees/acre Ft ³ volumes (ob and ib): total, to 2-, 3-, and 4-inch tops ob
Smith (1978)	Soils group Age A Dominant stand height	Trees/acre by dbh class and total tree height by dbh class Ft ³ volumes: total and merchantable to varying tops (ob) by dbh class and stand

Table A6.—Individual-tree model for plantations

Model	Inputs	Outputs
Daniels and Burkhart (1975)	Age A Number of trees/acre planted Site index (base age 25) Management choices: Spacing pattern Site preparation Thinning Fertilization	Number of trees/acre planted and surviving Average height of dominants and codominants Mean dbh Basal area and total ft ³ volumes ob

APPENDIX 4 COST STUDIES FOR TIMBERLAND TREATMENT

Table A7.—Timberland treatment cost studies by geographic area

Study	Year	Geographic area	Treatment ¹
Anderson and Granskog	1974	South (slash pine plantations in sandy soil on flat terrain)	Density
Cabbage and Granskog	1982	South (southern pine)	Density
Fight and Dutrow	1981	Southeast	Fertilization
Gardner	1981	South	Artificial reg.
Granskog	1978	South (slash pine)	Density
Granskog and Anderson	1980	South (loblolly pine)	Density
Guldin	1982, 1983	South (southern pine)	Artificial reg.
Hassler et al.	1981	South	Density
Kerr	1982	South	Artificial reg.
Lewis and Chappelle	1964	Virginia	Density
Mills et al.	1984	South	Artificial reg. density, other
Moak and Kucera	1975	Southern Coastal Plain, northern Coastal Plain, Piedmont	Artificial reg., density, other
Moak et al.	1977	Southern Coastal Plain, northern Coastal Plain, Piedmont	Artificial reg., density, other
Moak	1979	Southern Coastal Plain, northern Coastal Plain, Piedmont	Artificial reg., density, other
Moak et al.	1980	Southern Coastal Plain, northern Coastal Plain, Piedmont	Artificial reg., density, other
Moak	1982	South	Artificial reg., density, other
Row	1971	South	Artificial reg.
Schick and Maxey	1978	South	Density
Somberg et al.	1963	South	Artificial reg. density, other
Sunda and Lowry	1975	Texas, Louisiana, Arkansas	Artificial reg., density, other
Tufts et al.	1981	South	Equipment cost index
USDA Forest Service	1981a, 1981b	South	Artificial reg., density
Vasievich	1980	Southern Coastal Plain	Prescribed burning
Weaver and Osterhaus	1976	South (loblolly pine)	Artificial reg.
Worrell	1953	Southern Coastal Plain, northern Coastal Plain, Piedmont	Artificial reg., density, other
Yoho and Fish	1961	Southern Coastal Plain, northern Coastal Plain, Piedmont	Artificial reg., density, other
Yoho et al.	1969	Southern Coastal Plain, northern Coastal Plain, Piedmont	Artificial reg., density, other

¹See table 2 for description of timber treatment classes. "Other" refers to practices such as fire protection, marking trees for harvest, slash burning, and timber cruising.

Alig, Ralph J., Peter J. Parks, Robert M. Farrar Jr., and J. Michael Vasievich. 1984. Regional timber yield and cost information for the South: Modeling techniques. USDA Forest Service General Technical Report RM-112, 28 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

This report surveys analytical techniques for estimating the timber production of southern forests under various forestland management alternatives, and associated costs of those management alternatives. The integration of information from growth and yield modeling with timber management cost information in regional timber studies also is examined. Appendixes summarize the nature of data used to develop the timber growth and yield models, inputs required and outputs provided by the timber growth and yield models, and availability of cost information for different forestland management practices.

Keywords: Regional studies, timberland management, timber supply

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Rocky
Mountains



Southwest



Great
Plains

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Forest Service

Rocky Mountain Forest and Range Experiment Station

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United States
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Rocky Mountain
Forest and Range
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Fort Collins,
Colorado 80526

General Technical
Report RM-113



The Vegetation of Theodore Roosevelt National Park, North Dakota: A Habitat Type Classification

Paul L. Hansen, George R. Hoffman, and Ardell J. Bjugstad



Abstract

Vegetation of the Theodore Roosevelt National Park, North Dakota, was characterized according to habitat type based on concepts and methods developed by Daubenmire. Ten habitat types were described: seven—three grassland and four wooded types—occurred on upland plateaus, slopes, and relatively narrow benches along contours of the hills above the stream valleys; three—all wooded—occurred in valley bottoms. A key to identify the habitat types and discussion on the validation of the Habitat Type Classification and Species Diversity are provided.

Acknowledgements

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The Vegetation of Theodore Roosevelt National Park, North Dakota: A Habitat Type Classification

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Contents

	Page
STUDY AREA	1
Physiography and Soils	1
Climate	1
ECOLOGIC TERMS AND CONCEPTS	2
PREVIOUS VEGETATION STUDIES	2
METHODS	3
HABITAT TYPE DESCRIPTIONS	4
<i>Stipa comata</i> / <i>Carex filifolia</i> Habitat Type	4
<i>Agropyron smithii</i> / <i>Carex filifolia</i> Habitat Type	5
<i>Andropogon scoparius</i> / <i>Carex filifolia</i> Habitat Type	6
<i>Juniperus horizontalis</i> / <i>Andropogon scoparius</i> Habitat Type	7
<i>Artemisia tridentata</i> / <i>Agropyron smithii</i> Habitat Type	8
<i>Artemisia cana</i> / <i>Agropyron smithii</i> Habitat Type	9
<i>Fraxinus pennsylvanica</i> / <i>Symphoricarpos occidentalis</i> Habitat Type	11
<i>Fraxinus pennsylvanica</i> / <i>Prunus virginiana</i> Habitat Type	12
<i>Populus tremuloides</i> / <i>Betula occidentalis</i> Habitat Type	14
<i>Juniperus scopulorum</i> / <i>Oryzopsis micrantha</i> Habitat Type	15
<i>Symphoricarpos occidentalis</i> Community	15
KEY TO THE HABITAT TYPES	17
DISCUSSION	18
Validation of the Habitat Type Classification	18
Species Diversity	18
LITERATURE CITED	19
APPENDIX 1. Habitat Type Tables with Stand Data	21
APPENDIX 2. Tree Population Analyses	32
APPENDIX 3. Soil Analyses	34

The Vegetation of Theodore Roosevelt National Park, North Dakota: A Habitat Type Classification

Paul L. Hansen, George R. Hoffman, and Ardell J. Bjugstad

Increasing utilization of the northern Great Plains is reducing the areas of vegetation that are climax, or near-climax. Therefore, it becomes increasingly important to document in detail the vegetation characteristics of those areas currently free from, or only minimally disturbed by, human activities. Such areas are potentially valuable as reference areas against which to measure the impact of human activities. Theodore Roosevelt National Park (TRNP) in western North Dakota represents such a reference area, which also has a considerable diversity of habitats and vegetation types. This study documents the characteristics of pristine, or near-pristine, vegetation, and describes and delimits the habitat types (Daubenmire 1968) of TRNP. The information may be of interest to both those interested in basic ecological data and descriptions and those directly concerned with management of the vegetation described.

STUDY AREA

Physiography and Soils

Theodore Roosevelt National Park (TRNP) was established as a National Park in 1947. It covers 26,578 ha divided between the North and South Units (fig. 1). The area is part of the Missouri River Plateau and is unglaciated, except for a small portion of the North Unit, and even there, glacial deposits are not particularly evident. The substrates are stratified beds of soft shales, sandstones, and lignite of the Tertiary Tongue River Formation of the Fort Union Group (Laird 1950, 1956). These substrates have been severely dissected by the Little Missouri River and its tributaries, resulting in "badlands" topography of gullied ravines and valleys separated by interstream uplands of various dimensions, from large plateaus of many hectares to small buttes of erosion-resistant sandstone or scoria. Some of the buttes are 200 m above the valley floors. Exposed lignite has eroded along some of the steep hills, leaving resistant terraces paralleling the contours of the hills. At lower levels, just above the floodplains of the major streams, terraces of alluvium add another distinctive feature to the landscape. The region is physiographically complex, with various sites for the establishment and maintenance of vegetation types (fig. 2). The soils of TRNP are regosols belonging to the Bainville Series, developed from excessively drained, medium-textured, calcareous parent material (Omodt et al. 1968). A typical and obviously immature soil profile shows an A1 horizon overlying a C horizon. Textures range from loams to clay loams.

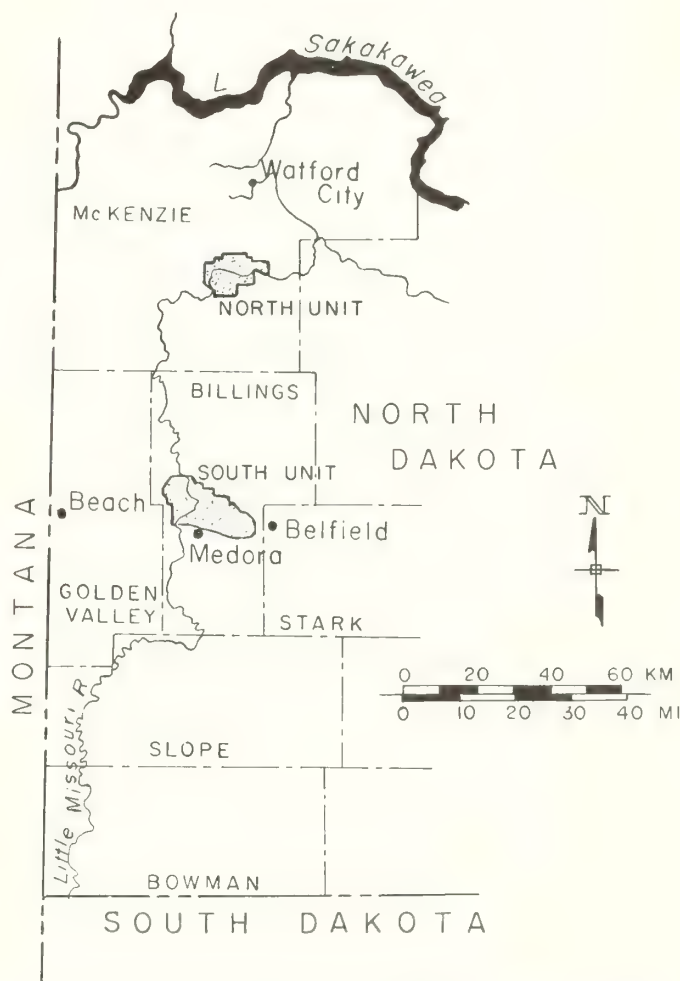


Figure 1.—Map of western North Dakota showing location of North and South Units of Theodore Roosevelt National Park.

Climate

The arid and continental climate of western North Dakota is characterized by long, cold winters and short, warm summers. The mean monthly low for January is -11.6°C , and the mean monthly high for July is 22.0°C . Most precipitation falls in early summer. June (the wettest month) precipitation ranges from mean 98.3 mm at Belfield to 83.6 mm at Medora (table 1). July means range from 72.6 mm at Belfield to 50.5 mm at Medora, illustrating the large decrease from June to July. The increase from May to June is equally impressive. Of the total precipitation in the region recorded at weather stations, 75% falls from April through September.



Figure 2.—General view of the landscape at TRNP showing the badland topography.

ECOLOGIC TERMS AND CONCEPTS

The following terms and concepts are consistent with usage proposed by Daubenmire (1968) and used in previous studies of habitat types (Daubenmire and Daubenmire 1968; Daubenmire 1970; Hoffman and Alexander 1976, 1980; Pfister et al. 1977; Mueggler and Stewart 1980). "Climax vegetation" is that which has attained a steady-state with its environment, such that species successfully maintain their population sizes. "Habitat type" is defined as the land area which supports or can support the same primary climax vegetation (Daubenmire 1968). The climax vegetation is referred to as a plant association. As an example, the *Artemisia tridentata*/*Agropyron spicatum* habitat type of south-central Washington state supports the plant association of the same name, under pristine conditions. Grazing, however, can alter significantly the species composition such that a community of *Artemisia tridentata*/*Bromus tectorum* can result. If the same plant association were burned, killing *Artemisia tridentata*, and grazed, removing *Agropyron spicatum*, the resulting plant community might become a *Poa secunda*/*Bromus tectorum* community. The habitat type does not change as long as the habitats retain the capability of supporting the *Artemisia*/*Agropyron* association (Daubenmire 1970). On normal soils and topography, the climax vegetation is referred to as a "climatic climax." Where slope and soil exert predominant influence on the microclimate, compared to that of normal topography, the climax vegetation may reflect the altered microclimate in both composition and structure. Such self-perpetuating vegetation, if significantly different from that on normal soils and topography, is referred to as a "topographic climax" or an "edaphic climax" or in some cases a "topoedaphic climax," where both slope and soil are important in altering the

climax vegetation. A "zootic climax" occurs where periodic grazing and trampling by domestic animals has altered the vegetation significantly. The altered vegetation maintains its composition and structure as a result of the kind and intensity of the periodic grazing. Seral vegetation is that which has not attained a steady-state with its environment. Ordinarily it follows a major disturbance.

Habitat types are defined to delimit and ecologically characterize land units of similar biotic potential, which makes the concept valuable to both basic and applied science. Habitat types can be useful in predicting rates of tree growth, susceptibility of trees to insects and mistletoe infection, potential for producing browse after fire, depth of soil moisture penetration, drought during the summer, and successional trends after disturbance (Arno and Pfister 1977; Daubenmire 1961, 1972; Hoffman and Alexander 1980, 1983; Layser 1974; Mueggler and Stewart 1980; Pfister 1972). The present study can provide a basis for better understanding the effects of grazing on habitat types in western North Dakota.

PREVIOUS VEGETATION STUDIES

Previous vegetation studies in western North Dakota did not include attempts to delimit habitat types. Hansor and Whitman (1938) described nine major kinds of grassland vegetation, which they correlated with edaphic and topographic factors. At least three of their types were considered to be seral, and the status of some others was not given. Their *Bouteloua gracilis* *Stipa comata*/*Carex filifolia* vegetation type on upland plateaus and gentle slopes, and the *Artemisia cana* *Agropyron smithii* vegetation type of alluvial flats adjacent the Little Missouri River and its tributaries were considered to be stable types. The *Andropogon gerardii*

Table 1.—Mean precipitation (P, in mm) and temperature (T, in °C) from selected weather stations near Theodore Roosevelt National Park

Month	Location							
	Beach		Belfield		Medora 3NNE		Watford City	
	P	T	P	T	P	T	P	T
Jan.	12.9	-11.1	15.7	-11.8	11.4	-11.9	14.5	-11.4
Feb.	10.4	-8.7	17.0	-8.4	12.7	-7.8	12.7	-9.4
Mar.	15.7	-2.9	22.1	-4.2	16.3	-3.3	19.8	-3.4
Apr.	30.5	5.5	32.5	5.1	25.9	5.7	34.0	6.1
May	55.4	11.7	55.9	11.9	44.2	12.6	48.0	12.9
June	90.2	16.8	98.3	16.3	83.6	17.2	86.9	17.3
July	44.2	20.9	72.6	20.1	50.5	21.2	52.6	21.8
Aug.	40.6	19.7	61.0	19.8	37.1	20.6	38.6	20.6
Sept.	31.5	13.8	30.7	13.6	30.7	14.1	33.3	14.4
Oct.	23.1	7.1	25.9	7.4	20.3	7.4	23.9	7.9
Nov.	12.7	-0.8	19.0	-1.6	14.2	-0.9	14.5	-1.7
Dec.	10.2	-7.2	8.6	-6.7	6.9	-6.9	13.2	-7.5
Annual ¹	377.4	5.4	459.3	5.1	353.8	5.7	392.0	5.7

¹ Mean total annual precipitation.

dominated type, much more restricted in distribution, also might have been stable (Hanson and Whitman 1938). Quinnild and Cosby (1958) found three apparently stable vegetation types on two ungrazed mesas in western North Dakota. The types were dominated by *Agropyron smithii*, *A. dasystachyum*, and *Stipa comata*, respectively. Larson and Whitman (1942) reported a vegetation type dominated by *Agropyron smithii*, *Bouteloua gracilis*, *Carex eleocharis*, and *C. filifolia* on an ungrazed mesa, in the badlands of South Dakota. From the badlands of southeastern Montana, Brown (1971) reported seven vegetation types dominated by the following: *Sarcobatus vermiculatus*, *Atriplex confertifolia*/*Artemisia tridentata*, *Artemisia tridentata*/*Atriplex confertifolia*-*Agropyron spicatum*, *Artemisia tridentata*/*Agropyron spicatum*, *Rhus trilobata*/*Agropyron spicatum*, *Juniperus scopulorum*/*Agropyron spicatum*, *Pinus ponderosa*/*Juniperus scopulorum*. The distribution of most of these vegetation types appeared to be controlled by specific soil and/or topographic characteristics. Ralston (1960) concluded that the lower temperatures and higher moisture levels of north-facing exposures at TRNP were primarily responsible for the success of *Juniperus scopulorum*-dominated vegetation there. Nelson (1961) described two additional forest types at TRNP, including a *Populus deltoides* vegetation type along streams, and a *Fraxinus pennsylvanica* vegetation type along streams and in upland ravines.

METHODS

The approach used follows that of Daubenmire and Daubenmire (1968) and Daubenmire (1970). Preliminary work at TRNP was done during the summer of 1978, by traveling extensively throughout the North and South Units, collecting plants and noting possible study sites. Stands of vegetation were sought that were nearly mature, most homogeneous, and least disturbed by fire, trails, past farming, or grazing. Homogeneity was an

important criterion and was determined subjectively. Obvious discontinuities and sharp breaks in the microtopography of any stand, and locally disturbed areas, such as animal trails, were avoided. Areas in stands were chosen which appeared to have a representative expression of all vegetation layers present. From the 1978 field work, a tentative list was made of the habitat types to be substantiated or altered as a result of intensive sampling in 1979.

During the summer of 1979, 70 stands were intensively sampled. At each stand sampled, a rectangular plot 15 x 25 m was set up. If the plot was located on a slope, it was oriented with the long axis parallel to the contour to maximize the chance of remaining within the same soil type. In woodland stands, sample plots were selected to include the largest trees of the stand, provided the trees were not located near trails, ecotones, or other disturbances. With the largest trees possible in each 375-m² plot, the undergrowth vegetation and soil were most representative of the oldest part of the stand. Each plot was then subdivided into three 5 x 25 m macroplots. Within each 375-m² plot, all trees taller than 1 m were measured at breast height and were recorded in diameter size classes. Trees shorter than 1 m were counted in two 1 x 25 m strips along the sides of the central macroplot. In the calculation of tree basal areas, the midpoints of the diameter classes were used. Because the largest trees in the plots were included, the basal area calculation produced a higher basal area than would be expected for the average stand. The technique was used consistently throughout the study, so that the results could be compared from one stand to another.

In each stand sampled, canopy coverages were estimated for all undergrowth species within 50 2 x 5 dm microplots placed systematically along the sides of the central macroplot. The canopy coverage of each species was recorded as one of six coverage classes: 1 = <1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, 6 = 96-100% (Daubenmire 1959). Mosses and lichens were lumped together for coverage

estimates. Plant species in the 15 x 25 m plots which occurred in none of the 2 x 5 dm microplots were noted also.

In each stand, 25 samples of the upper decimeter of mineral soil were collected. The samples were air-dried in the field, then were composited for laboratory analysis. Soil passing through a 2-mm sieve was used to determine texture using a modified Bouyoucos method, pH using a combination electrode on the saturated soil paste, nitrogen by the Kjeldahl method, and organic matter by a modified Walkley-Black method (Moodie and Koehler 1975). Cation exchange capacity (C.E.C.), free lime, and extractable cations were determined using appropriate Hach Chemical test kits.

Nomenclature for plants collected in this study follows Van Bruggen (1976). Where possible, identification was carried out to the species level. Although plants were collected at various times during the growing season, there were some taxonomic difficulties related to the lack of flowering specimens or to the lack of clear taxonomic differences among certain species. As a result, the following were combined: (1) *Viola* spp., which includes *V. adunca*, *V. canadensis*, *V. nuttallii*, *V. pedatifida*, and *V. pratensis*; (2) Polypodiaceae, which includes *Cystopteris gracilis* and *Woodsia oregana*; (3) *Astragalus* sp., which is probably *A. adsurgens*; and (4) *Ribes setosum*, which could include *Ribes oxycanthoides*. Voucher specimens collected in this study were deposited at TRNP and in the herbarium at the University of South Dakota.

HABITAT TYPE DESCRIPTIONS

Stipa comata/*Carex filifolia* Habitat Type

This habitat type occurs on upland plateaus and gentle slopes that appear to be free of excessive erosion (fig. 3). Seven stands were sampled; 49 species were recorded (table A1). *Stipa comata*, *Carex filifolia*, *Agropyron smithii*, *Koeleria pyramidata*, and *Selaginella densa* provide the greatest coverage (table A1). *Stipa comata* forms the dominant union (Daubenmire 1968) of this association. Its abundance and stature is usually indicative of the association. During years of low moisture, *Stipa comata* produces short plants with only a few flowering culms. Close inspection of the vegetation reveals a relatively complex structure, with grasses and broadleaf forbs forming a union under *Stipa*. *Agropyron smithii* dominates this union; other conspicuous members include *Koeleria pyramidata*, *Artemisia dracunculus*, *Chrysopsis villosa*, *Lactuca oblongifolia*, *Lygodesmia juncea*, and *Tragopogon dubius*. Another union of this association is dominated by *Carex filifolia*, which has 28.5% coverage. Other important species of this low-growing union are *Artemisia frigida*, *Carex eleocharis*, *Bouteloua gracilis*, and *Gaura coccinea*. This union provides 40–50% coverage wherever it occurs in the study region. Very close to the ground surface, and in places forming dense mats, is *Selaginella densa*, which provides 47.6% coverage in this association. Outside



Figure 3.—The *Stipa comata*/*Carex filifolia* habitat type occurs on uplands where the soil is deep and well-drained. The meter stick used for scale in this and subsequent photos is painted in decimeter segments.

this association, *Selaginella densa* occurs only rarely. The *Stipa/Carex* association is the apparent climatic climax of this study region.

Major species with their constancy and mean coverage percentages are the following:

Species	Constancy	Mean coverage
<i>Stipa comata</i>	100	39.4
<i>Carex filifolia</i>	100	28.5
<i>Bouteloua gracilis</i>	86	0.9
<i>Carex eleocharis</i>	100	1.3
<i>Agropyron smithii</i>	75	10.3
<i>Koeleria pyramidata</i>	100	9.7
<i>Artemisia frigida</i>	100	3.1
<i>Gaura coccinea</i>	86	0.7
<i>Lactuca oblongifolia</i>	86	4.0
<i>Lygodesmia juncea</i>	71	0.9
<i>Tragopogon dubius</i>	100	0.4
<i>Selaginella densa</i>	100	47.6
<i>Artemisia dracunculus</i>	100	2.7

Compared to some of the other habitat types, forbs are relatively more important, although graminoids provide the greatest coverage. Among the seven stands sampled, the mean coverages of graminoids, forbs, and shrubs are the following:

graminoids: mean coverage = 90%; S.E. = 9.46
 forbs: mean coverage = 62.4%; S.E. = 7.82
 shrubs: mean coverage = 3.29%; S.E. = 0.71.

Forb coverage is almost 70% that of the graminoids. Hanson and Whitman (1938) reported a community in western North Dakota dominated by *Bouteloua gracilis*, *Stipa comata*, and *Carex filifolia*. They suggested this community closely reflected the macroclimate of the region. Coupland (1950, 1961) described a *Stipa comata-Bouteloua gracilis* community in western Canada in which *Carex filifolia* is important and in which *Stipa comata* is a productive species. He reported *Carex filifolia* increases in abundance in a southerly direction from Canada, and with overgrazing, *Bouteloua gracilis* becomes a dominant species. Nelson (1961) reported that heavy grazing favors the "short" grasses over the "midgrasses." In the present study, *Bouteloua gracilis* contributed little to the total canopy coverage. Coupland (1950, 1961) also found *Selaginella densa* to be an important component of the *Stipa comata*-dominated community, and suggested that *Selaginella densa* increases with protection from grazing and decreases from trampling by grazing animals on some Canadian grasslands. Mueggler and Stewart (1980) reported a *Stipa comata/Bouteloua gracilis* habitat type on alluvial substrates in southern Montana, mainly east of the Continental Divide. Their data suggest it is the most xeric steppe habitat type in western Montana. This habitat type has some similarities to the *Stipa/Carex* habitat type of TRNP, although the latter is considerably richer floristically.

Soils of this habitat type range from sandy loams to loamy sands. The high sand content of soils of *Stipa*

comata-dominated vegetation corresponds to other findings (Coupland 1961, Daubenmire 1970, Dix 1960, Hanson 1935, Hanson and Whitman 1938, Lauenroth and Whitman 1977, and Wright and Wright 1948). Sandy soils in this climate have a high infiltration rate, deep penetration of water, and high moisture availability, but low moisture-holding capacity. The organic matter contents of these soils were lowest of all the soils in this study and may be related to coarse textures. They readily leach, have high oxidation rates, and possibly low productivity. Edaphic characteristics are given in Appendix 3.

Agropyron smithii/Carex filifolia Habitat Type

This habitat type occurs on slopes of 9% to 20%, and is characterized by the dominance of *Agropyron smithii* and *Carex filifolia* (fig. 4). In the nine stands sampled, only 32 species occurred, compared to 49 species of the *Stipa comata/Carex filifolia* habitat type (table A2). Constancy and mean coverage percentages of the major plants of the nine stands sampled are as follows:

Species	Constancy	Mean coverage
<i>Agropyron smithii</i>	100	91.2
<i>Carex filifolia</i>	78	14.0
<i>Artemisia frigida</i>	78	1.1
<i>Tragopogon dubius</i>	78	0.2
<i>Stipa comata</i>	67	1.2
<i>Lactuca oblongifolia</i>	56	0.4

Forbs are particularly underrepresented in this habitat type. The importance of graminoids in this habitat type may be illustrated by examining the total coverage provided compared to that of the forbs and shrubs. The mean total graminoid coverage of the nine stands sampled was 111.7% (S.E. = 4.01), and the mean total forb coverage in the same nine stands was 2.33% (S.E. = 0.91). Shrubs also provided little coverage in these stands; mean total shrub coverage was 1.44% (S.E. = 0.38).

The soils of this habitat type are fine-textured. Hanson and Whitman (1938) described a plant community in western North Dakota dominated by *Agropyron smithii*, *Bouteloua gracilis*, and *Carex filifolia*, which occurred on gradual slopes of heavy-textured soils. Quinnild and Cosby (1958) found vegetation of mesa tops in western North Dakota dominated by *Agropyron smithii*, *Agropyron dasystachyum*, *Stipa comata*, *Bouteloua gracilis* and *Artemisia frigida*. Larson and Whitman (1942) also reported on *Agropyron smithii*-dominated vegetation on mesas in the badlands of South Dakota. Their results suggest protection maintains a vegetation type dominated by *Agropyron smithii* and *Carex* sp., while combined mowing and grazing produces vegetation dominated by *Bouteloua gracilis*.

All surface soils of this habitat type were classified as loams; the clay content ranged from 14.0% to 24.4%. Fine-textured soils in this semiarid region have poor water balance conditions. This may account for the less



Figure 4.—Long slope of fine-textured soil which supports the *Agropyron smithii*/*Carex filifolia* habitat type.

rich assortment of species though *Agropyron smithii* is favored and often occurs in dense stands on heavy soils in this region (Weaver and Albertson 1956). The *Agropyron*/*Carex* association at TRNP is an edaphic climax.

***Andropogon scoparius*/*Carex filifolia* Habitat Type**

Nine stands of this habitat type were sampled. A total of 66 species, including nine shrub species, were found. This habitat type is characterized by the dominance of *Andropogon scoparius* (fig. 5) with a mean coverage of 76.8% (table A3).

Characteristic species of this habitat type with constancy and mean coverage percentages are the following:

Species	Constancy	Mean coverage
<i>Andropogon scoparius</i>	100	78.8
<i>Calamovilfa longifolia</i>	100	5.3
<i>Carex filifolia</i>	100	8.8
<i>Koeleria pyramidata</i>	89	0.7
<i>Echinacea angustifolia</i>	89	0.6
<i>Aster oblongifolius</i>	89	0.4
<i>Artemisia frigida</i>	89	0.4
<i>Helianthus rigidus</i>	78	3.6
<i>Lactuca oblongifolia</i>	67	1.0
<i>Gaura coccinea</i>	67	0.5
<i>Lygodesmia juncea</i>	67	0.2

Although forbs provide limited coverage, there are numerous species which add considerable diversity to

the vegetation of this habitat type. The mean coverages of graminoids, forbs, and shrubs in stands of this habitat type are as follows:

graminoids:	mean coverage = 97.4%;	S.E. = 2.86
forbs:	mean coverage = 7.78%;	S.E. = 2.59
shrubs:	mean coverage = 1.22%;	S.E. = 0.41

Although more forb and shrub species are present in this habitat type, both life forms provide much less coverage than in the *Stipa*/*Carex* habitat type.

Because of the topographic position and the coarse-textured soils generally associated with the stands studied, the vegetation is considered to be a topoedaphic climax.

Hanson and Whitman (1938) described an *Andropogon scoparius*-dominated community on northerly slopes and where snow accumulates. They observed that *Andropogon* colonized bare areas created by step erosion. Once established, it spread and continued to dominate larger eroded areas, and its density and height made it an effective competitor with shorter species. The stands of *Andropogon*/*Carex* habitat type studied also may have become established after erosion. They appear to be permanent; there is no evidence other species are replacing the *Andropogon*. Redmann (1975) described a community dominated by *Andropogon scoparius*. His stands were on north-facing slopes, and both *Helianthus rigidus* and *Rosa arkansana* were important species.



Figure 5.—Well-developed stand of *Andropogon scoparius*/*Carex filifolia* association.

Both Hanson and Whitman (1938) and Redmann (1975) observed small stands of *Andropogon gerardii*-dominated vegetation. The present study also found small stands of vegetation, usually on steep south-facing slopes and primarily in the North Unit. These stands are small and are not considered sufficiently large to sample or to classify as a habitat type.

Soils of this habitat type have high sand and low clay contents. In three of the stands studied, soils had considerable gravel, from 7% to 36% by weight. In the South Unit of TRNP, the five stands sampled were on soils rich in gravel or scoria, on slopes ranging from 18% to 42%. In the North Unit of TRNP, this habitat type is restricted primarily to the glaciated areas north of the Missouri River, though a few stands were observed south of the River, in the Achenbach Hills region. Stands 22, 23, and 24 had gravel ranging from 6.7% to 36.2% of the soil dry weight. Edaphic characteristics are given in Appendix 3.

***Juniperus horizontalis*/*Andropogon scoparius* Habitat Type**

Five stands of this vegetation were sampled; all are in the South Unit of the Park and on slopes exceeding 28%. This habitat type is distinguished by the dominance of *Juniperus horizontalis*, with a mean coverage of 80.4%, and the presence of the *Andropogon scoparius* union (fig. 6). The *Carex filifolia* union is also represented (table A4). In the stands sampled, there were 60 species, 43 of which also occur in the *A. scoparius*/*C. filifolia*

habitat type (table A4). Based on a floristic comparison, the *Andropogon*/*Carex* and *Juniperus*/*Andropogon* habitat types are 68% similar. Ten shrub species occur in the *Juniperus*/*Andropogon* habitat type, although the coverage of *J. horizontalis* exceeds considerably the combined coverage of all the other shrubs. Stand 10 was richest with eight shrub species, including *J. horizontalis*, *Artemisia cana*, *Potentilla fruticosa*, *Prunus virginiana*, *Rhus aromatica*, *Rosa arkansana*, *Shepherdia argentea*, and *Symphoricarpos occidentalis*. There, the coverage of *J. horizontalis* was 83%, and the total coverage of the remaining seven shrubs was 30%. This habitat type is rather localized in its distribution. On the basis of topographic and edaphic factors, vegetation of this habitat type is a topoedaphic climax. Major species with their constancy and mean coverage percentages in this association are as follows:

Species	Constancy	Mean coverage
<i>Juniperus horizontalis</i>	100	80.4
<i>Andropogon scoparius</i>	100	24.2
<i>Calamovilfa longifolia</i>	100	7.0
<i>Carex filifolia</i>	100	3.0
<i>Campanula rotundifolia</i>	100	1.1
<i>Petalostemon purpureum</i>	100	0.6
<i>Galium boreale</i>	80	4.8
<i>Anemone patens</i>	80	2.4
<i>Potentilla fruticosa</i>	80	2.4
<i>Gaura coccinea</i>	80	0.6
<i>Echinacea angustifolia</i>	80	0.5
<i>Linum perenne</i>	80	0.3
<i>Senecio plattensis</i>	80	0.2

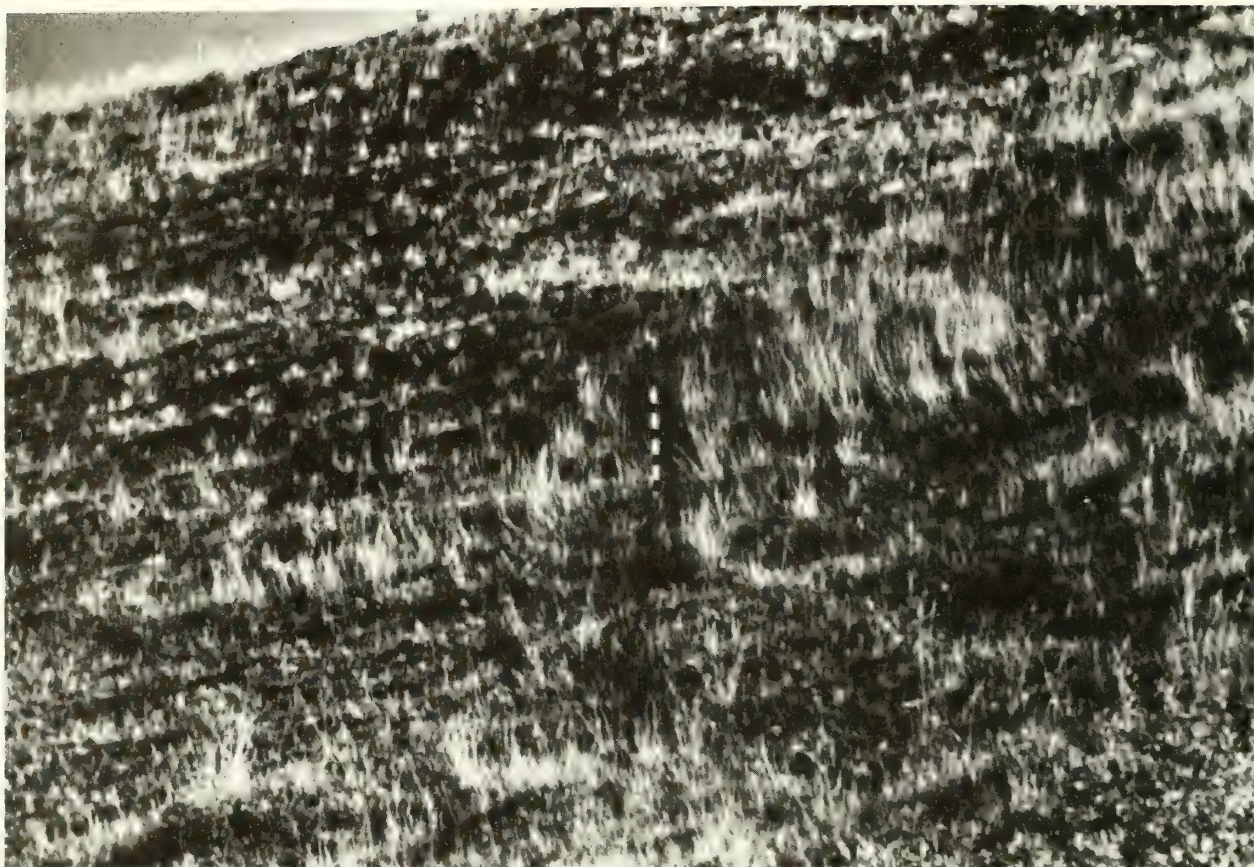


Figure 6.—*Juniperus horizontalis*/*Andropogon scoparius* habitat type. The low-growing *Juniperus* is evident as a low growing, darker plant in this photo. Scattered culms of *Andropogon* are also conspicuous.

Of these 13 species with high constancies, only five have 67% or higher constancies in the *Andropogon*/*Carex* association. Comparing the lists of species with high constancy values for the *Andropogon*/*Carex* and *Juniperus*/*Andropogon* associations, the floristic similarity is only 38%, considerably lower than the similarity based on the total species lists of both associations. Coupland (1961) reported *J. horizontalis* on exposed sites in the Great Sand Hills, Alberta. Quinnild and Cosby (1958) found it on eroded edges of a mesa in western North Dakota. Whitman and Hanson (1939) described a community on scoria buttes in North Dakota, in which both *J. horizontalis* and *Mentzelia decapetala* were dominant. Redmann (1975) observed occasional mats of *J. horizontalis* on sandy soil in western North Dakota. At TRNP, stands of *J. horizontalis* appear to be stable, and habitat type status is assigned to these sites. Edaphic characteristics of this habitat type are listed in Appendix 3.

***Artemisia tridentata*/*Agropyron smithii* Habitat Type**

This habitat type occurs on terraces or narrow benches that parallel the contours of hills 10 to 60 m above the valley floor of the Little Missouri River and its principal tributaries (fig. 7). In the four stands of this

vegetation, only 29 species were found. *Artemisia tridentata* is dominant, and both the *Agropyron smithii* and *Carex filifolia* unions are represented (table A5). There are nine shrub species, but the coverage of *A. tridentata* far exceeds the combined coverage of the remaining eight shrubs. *Atriplex confertifolia* is second with slightly less than 2% mean coverage. The paucity of species reflects the severity of the habitats supporting this vegetation, which is also a topoedaphic climax. Major species of this association and their constancy and mean coverage percentages are as follows:

Species	Constancy	Mean coverage
<i>Artemisia tridentata</i>	100	29.7
<i>Agropyron smithii</i>	100	68.8
<i>Agropyron caninum</i>	100	8.1
<i>Opuntia polyacantha</i>	100	0.4
<i>Atriplex confertifolia</i>	75	1.5
<i>Carex filifolia</i>	50	3.2

All species of the four stands studied are listed in table A5. Shrubs and graminoids are most conspicuous in this habitat type; forbs are sparse. The mean coverages of shrubs, graminoids, and forbs are as follows:

shrubs:	mean coverage = 33.5%;	S.E. = 4.35
graminoids:	mean coverage = 83.0%;	S.E. = 8.83
forbs:	mean coverage = 3.5%;	S.E. = 1.71



Figure 7.—*Artemisia tridentata*/*Agropyron smithii* habitat type This habitat type occurs on narrow benches or terraces along the contours of the hills.

Edaphic characteristics of the four stands studied are listed in Appendix 3.

Other descriptions of *Artemisia tridentata*-dominated vegetation of western North Dakota and eastern Montana indicate broad similarities in composition and habitat conditions (Brown 1971, Hazlett and Hoffman 1975, Whitman and Hanson 1939). In the Missouri River "breaks" region of Montana, Mackie (1970) described an *Artemisia tridentata*/*Agropyron smithii* association as an edaphic climax on "shallow, gravelly, or claypan surface soils."

In his study of badland vegetation in southeastern Montana, Brown (1971) described a community dominated by *Artemisia tridentata*, with *Atriplex confertifolia* and *Agropyron spicatum* as codominants. *Agropyron smithii* was present in small patches.

***Artemisia cana*/*Agropyron smithii* Habitat Type**

This habitat type occurs on large areas of floodplains and river terraces adjacent the Little Missouri River and its tributaries, areas commonly referred to as "sagebrush flats" (fig. 8). The dominant is *Artemisia cana*, with a mean coverage of 33.6% (table A6). Between widely spaced shrubs, numerous other species occur in one or two lower unions dominated by *Agropyron smithii* and *Carex filifolia*. Although 55 species occurred in the 12 stands sampled, only seven have a constancy of 50% or higher. Major species of this

association and their constancy and mean coverage percentages are as follows:

Species	Constancy	Mean coverage
<i>Artemisia cana</i>	100	33.6
<i>Agropyron smithii</i>	100	70.9
<i>Stipa viridula</i>	75	2.4
<i>Agropyron caninum</i>	67	6.6
<i>Artemisia frigida</i>	58	0.6

As in the *Artemisia tridentata*/*Agropyron smithii* habitat type, graminoids in this habitat type provide considerably more coverage than either forbs or shrubs. The total forb and shrub coverage in this habitat type, however, is greater than in the *A. tridentata*/*A. smithii* habitat type. The means for this habitat type are the following:

shrubs:	mean coverage = 54.1%;	S.E. = 7.69
graminoids:	mean coverage = 84.8%;	S.E. = 5.32
forbs:	mean coverage = 9.4%;	S.E. = 2.27.

Floristically, this habitat type is only 47% similar to that of the *A. tridentata*/*A. smithii* habitat type. *Symphoricarpos occidentalis* occurs in five of the stands sampled; its mean coverage is 47%. Clones of this species are described in detail later. *Agropyron caninum* and *Muhlenbergia cuspidata* reach their maximum abundance in this and the *A. tridentata*/*A. smithii* habitat type.



Figure 8a.—*Artemisia cana*/*Agropyron smithii* habitat type. The relatively wide spacing of *Artemisia* and nearly complete herbaceous cover is evident in this photo.



Figure 8b.—Broad level deposit of alluvium support *Artemisia cana*-dominated vegetation. These areas are referred to as "sagebrush flats."

This vegetation is heavily utilized by bison and deer in TRNP. Nelson (1961) suggested that heavy grazing of this vegetation reduces the amounts of *A. smithii* and *Stipa viridula* in favor of *Bouteloua gracilis*. Hanson and Whitman (1938) suggested that occasional flooding and deposition of alluvium might prevent short grasses from becoming important in this vegetation. *A. cana* provides fall and winter browse for game animals and, outside TRNP, for livestock (Johnson and Nichols 1970).

The substrates vary considerably with respect to drainage and texture, and have moderate salt content (Hanson and Whitman 1938). The *A. cana*/*A. smithii* association is an edaphic climax in this region.

This is an important habitat type, covering large areas. Outside the Park, grazing animals utilize it heavily, and ungrazed stands of the habitat type inside the Park become even more valuable as reference areas. Edaphic characteristics are listed in Appendix 3.

***Fraxinus pennsylvanica*/*Symphoricarpos occidentalis* Habitat Type**

In the arid northern Great Plains, woodland vegetation is confined to habitats where adequate soil moisture, along streams or in other favorable topographic positions, compensates for the arid climate (fig. 9). The

F. pennsylvanica/*S. occidentalis* association is an edaphic climax on the floodplain adjacent the Little Missouri River and its major tributaries. Tree population data for this habitat type are given in Appendix 2. *Populus deltoides* currently dominates many of the stands but is no longer reproducing. The data indicate it will be replaced by *Fraxinus pennsylvanica*. Tree basal areas of the stands studied range from 23.3 m²/ha to 63.1 m²/ha (Appendix 2). The larger trees, some 6–7 dm d.b.h., are *Populus deltoides*, but the young trees establishing in the stands are *Fraxinus pennsylvanica*. *Juniperus scopulorum* is tallied with the tree species in the data, although it is an understory species in the closed forest. Its current abundance is attributed to adequate light penetrating to the shrub and herb layers of the community as a result of wide spacing of the old *Populus*. Along the Missouri River, in central North Dakota (Burgess et al. 1973), in southeastern South Dakota (Wilson 1970), and near Omaha, Nebr. (Vaubel 1975), *Populus deltoides* is a pioneer species, and is replaced successionally by various combinations of *Fraxinus*, *Ulmus*, *Acer*, and *Celtis*. The *F. pennsylvanica*/*S. occidentalis* habitat type is recognized by the combination of tree and undergrowth unions. *F. pennsylvanica* is present in the understory, although the overstory may be dominated currently by the non-reproducing *Populus deltoides*. The undergrowth is dominated by the Sym-

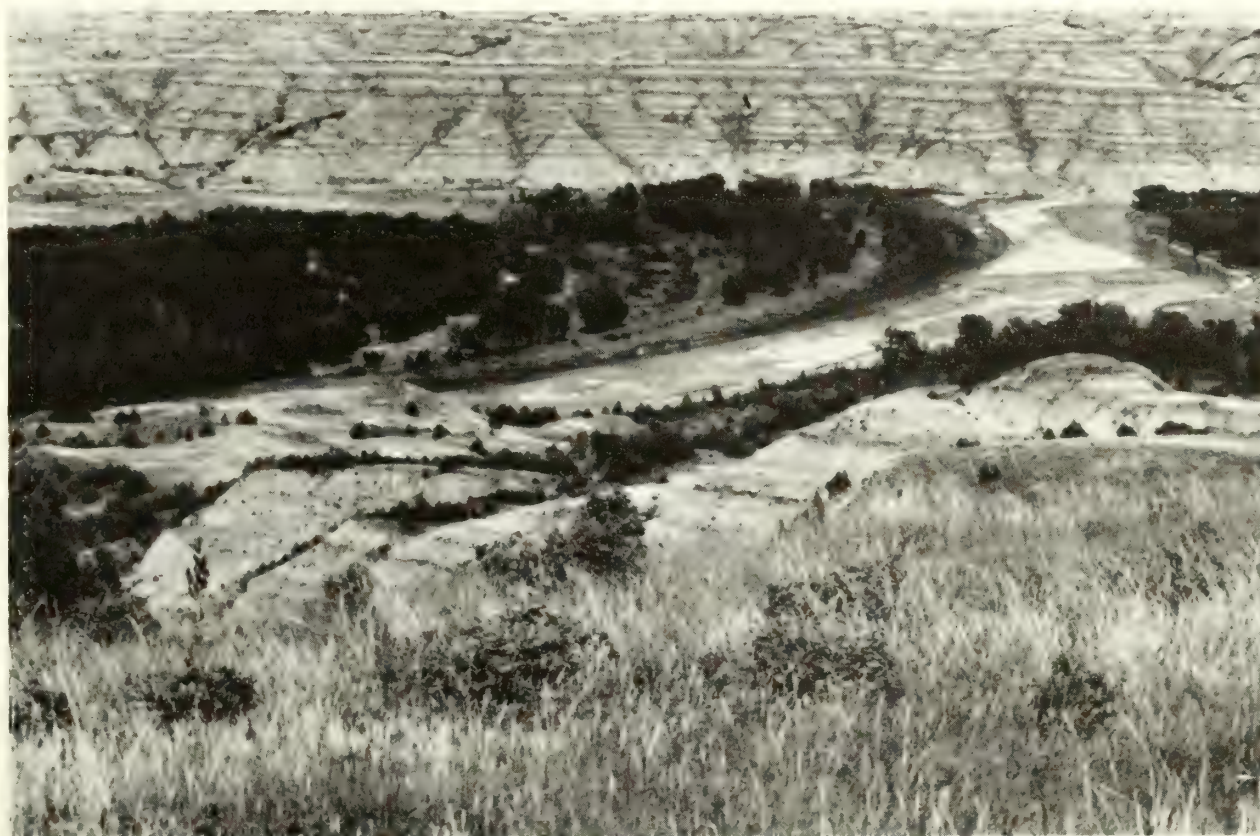


Figure 9.—The *Fraxinus pennsylvanica*/*Symphoricarpos occidentalis* habitat type is confined in this semiarid climate to relatively narrow bands paralleling larger streams. Along a meander of the Little Missouri River, shown here, *Populus deltoides* became established in rows parallel to the stream course.

phoricarpus occidentalis union with *S. occidentalis*, *Rhus aromatica*, *Toxicodendron rydbergii*, and other shrubs well-represented (fig. 10). Among the grasses, *Calamovilfa longifolia*, *Elymus canadensis*, and *Muhlenbergia racemosa* are important (table A7). In the four stands sampled, there are 52 undergrowth species. Major undergrowth species of the stands sampled and their constancy and mean coverage percentages are as follows:

Species	Constancy	Mean coverage
<i>Symphoricarpus occidentalis</i>	100	40.5
<i>Toxicodendron rydbergii</i>	100	23.0
<i>Melilotus officinalis</i>	100	28.8
<i>Elymus canadensis</i>	100	11.5
<i>Muhlenbergia racemosa</i>	100	8.3
<i>Melilotus albus</i>	100	7.0
<i>Rhus aromatica</i>	100	5.4
<i>Agropyron caninum</i>	100	4.0
<i>Smilacina stellata</i>	100	0.9
<i>Parthenocissus vitacea</i>	100	0.6
<i>Poa pratensis</i>	75	37.2

The importance of shrubs, graminoids, and forbs may be shown by their mean coverage values:

shrubs:	mean coverage = 76.8%;	S.E. = 23.2
graminoids:	mean coverage = 64.2%;	S.E. = 27.0
forbs:	mean coverage = 43.5%;	S.E. = 15.8.

Symphoricarpus and *Toxicodendron* together provide 63.5% coverage among the shrubs.

Before TRNP excluded cattle, grazing was common in these streamside forests. Currently, in TRNP, bison sometimes utilize this habitat type for grazing, watering, and the shade provided during the summer. The importance of certain alien species attests to the heavy usage earlier by cattle, and the considerable usage by bison now that the area is a National Park. The most important grass is *Poa pratensis*, with a mean coverage of 36.2%. The most important forb is *Melilotus officinalis*, with a mean coverage of 28.8%. Edaphic characteristics of stands sampled are listed in Appendix 3.

***Fraxinus pennsylvanica*/*Prunus virginiana* Habitat Type**

This habitat type occurs in ravines or draws or on moderately steep north-facing slopes throughout much of TRNP. It is recognized by the presence of *Fraxinus pennsylvanica* as the dominant species, with *Ulmus americana* as a codominant in some of the stands. Both species reproduce successfully in this habitat type. In V-shaped ravines, largest *Fraxinus* occur near the center, or bottom, of the stand, where there is greater soil moisture. Tree basal area of the stands studied ranged from 21.6 m²/ha to 35.9 m²/ha (Appendix 2). The largest tree sampled was a *Fraxinus*, with 116 xylem rings at breast height. The average age of the *Fraxinus*



Figure 10.—Interior of a stand of the *Fraxinus pennsylvanica*/*Symphoricarpus occidentalis* habitat type. The undergrowth here is a rich mixture of both shrubs and herbaceous species, with *Fraxinus* seedlings obvious in the foreground.

was 60–70 years. Heart rot prevented determining the age of some of the larger *Fraxinus*. *Ulmus americana* is important in some stands, and *Acer negundo* and *Juniperus scopulorum* also occur in this habitat type. The undergrowth is dominated by *Prunus virginiana*, 2–3 m tall, with a mean coverage of 27.7% (fig. 11). This shrub reaches its greatest density near the edge of these stands, where light intensity is greater, and it often forms a fringe beyond the stand margin. The smaller *Symphoricarpos occidentalis* and *Rosa woodsii* are also important shrubs in the undergrowth (table A7). The important graminoids of this habitat type are *Carex sprengelii*, with a mean coverage of 61.1%, and *Elymus virginicus*, with a mean coverage of 27.5%. These two species reach their maximum importance in this habitat type. Owing to heavy utilization by cattle in the past, and possibly as a result of bison use currently, *Poa pratensis* and *Taraxacum officinale* are both important in this habitat type. Tree seedlings and saplings are abundant; trampling by bison apparently is not an important factor at present. *Galium boreale*, with a mean coverage of 10.2%, is the most important forb. Other forbs characteristic of this habitat type include *Monarda fistulosa*, *Thalictrum dasycarpum*, *T. venulosum*, *Sanicula marilandica*, *Arctium minus*, and *Ranunculus abortivus*. In the four stands sampled, 51 species were found. The vegetation appears to be a topographic climax. Important undergrowth species in stands of this habitat

type and their constancy and mean coverage percentages are as follows:

Species	Constancy	Mean coverage
<i>Prunus virginiana</i>	100	27.7
<i>Symphoricarpos occidentalis</i>	100	12.1
<i>Elymus virginicus</i>	100	27.5
<i>Galium boreale</i>	100	10.2
<i>Carex sprengelii</i>	50	30.6
<i>Poa pratensis</i>	75	15.6

Mean coverages for shrubs, graminoids, and forbs are as follows:

shrubs:	mean coverage = 46.2%;	S.E. = 14.0
graminoids:	mean coverage = 82.2%;	S.E. = 19.0
forbs:	mean coverage = 29.0%;	S.E. = 11.6.

Compared to the *Fraxinus*/*Symphoricarpos* habitat type, graminoids provide greater coverage, but both shrubs and forbs provide less coverage. Overall, the total mean undergrowth coverage is 157.4% for the *Fraxinus*/*Prunus* habitat type, compared to 184.5% for the *Fraxinus*/*Symphoricarpos* habitat type. Stands of this habitat type are important deer habitats, providing both browse and shelter. Stands also attract domestic grazing animals outside the boundary of TRNP. Lack of tree



Figure 11.—*Fraxinus pennsylvanica*/*Prunus virginiana* habitat type. Photo taken from the edge of the stand. *P. virginiana* dominates the undergrowth.

reproduction in such stands have concerned other investigators (Boldt et al. 1978, Severson and Boldt 1978). It appears from their studies, and also from results of a study in the Custer National Forest, that cattle grazing and trampling is the most important single cause of failure of trees to successfully replace themselves in these wooded draws. The stands in TRNP become all the more important, therefore, as reference areas with which to compare changes resulting from domestic animal activity outside the Park. Even within the Park, considerable variation in undergrowth vegetation among stands of this habitat type reflect the effects of grazing before the area was a national park.

Edaphic characteristics of stands of this habitat type are given in Appendix 3.

Populus tremuloides/Betula occidentalis Habitat Type

This habitat type occurs on upper slopes facing northwest to east (fig. 12). Stands of the *Fraxinus/Prunus* habitat type are lower on the same slopes. The habitat type is not widespread in TRNP, and is recognized by the dominance of *Populus tremuloides*. The vegetation is also a topographic climax. The undergrowth is dominated by *Betula occidentalis*, with a mean coverage of 22.1%, *Prunus virginiana*, with a mean coverage of 31.1%, and *Symphoricarpos albus*, with a mean coverage of 20.5%. *S. occidentalis* and *Toxicodendron*

rydbergii are also important undergrowth shrubs in this habitat type. *Carex sprengeii*, *Oryzopsis micrantha*, and *Apocynum androsaemifolium* are major herbaceous species in this habitat type, with *Disporum trachycarpum*, *Galium boreale*, and *Smilacina stellata* also important. In the four stands sampled, 57 species were encountered (table A7). Mean basal area of trees in stands sampled is 24.6 m²/ha. The largest size class represented among the tree species is 2-3 dm d.b.h. The largest *Populus*, based on xylem layers at breast height, ranged from 43 to 77 years. Major undergrowth species in stands of this habitat type and their constancy and mean coverage percentages are as follows:

Species	Constancy	Mean coverage
<i>Betula occidentalis</i>	100	22.1
<i>Prunus virginiana</i>	100	31.1
<i>Toxicodendron rydbergii</i>	100	22.7
<i>Disporum trachycarpum</i>	100	5.4
<i>Smilacina stellata</i>	100	3.6
<i>Galium boreale</i>	100	5.0
<i>Apocynum androsaemifolium</i>	75	11.4

Graminoids provided less coverage in this habitat type than in any other habitat type studied. Mean coverages for shrubs, graminoids, and forbs in stands sampled are as follows:



Figure 12.—*Populus tremuloides/Betula occidentalis* habitat type. Undergrowth is a rich mixture of shrubs and forbs primarily.

shrubs:	mean coverage = 91.5%;	S.E. = 14.2
graminoids:	mean coverage = 20.8%;	S.E. = 9.1
forbs:	mean coverage = 43.2%;	S.E. = 8.9.

Shrub coverage is higher than that of other habitat types, and forb coverage is the same as that of the *Fraxinus/Symphoricarpos* habitat type but higher than that of the *Fraxinus/Prunus* habitat type. There is a 46% floristic similarity between stands of this habitat type and those of the *Fraxinus/Prunus* habitat type. The *Fraxinus/Prunus* and *Populus/Betula* habitat types are in relatively close proximity; and although they share nearly half their species, the two habitat types are distinct and can be separated on the basis of critical overstory and undergrowth species.

As shown in Appendix 2, the tree stratum in stands of this habitat type has six species, although seldom do all occur in the same stand. Both *P. tremuloides* and *F. pennsylvanica* have population structures indicating successfully reproducing species that could maintain or increase their population sizes. *Fraxinus* is currently a codominant in this habitat type; but it may become a more important species in the future. A constant source of seeds is available from lower slope stands of the *Fraxinus/Prunus* habitat type. Edaphic characteristics are given in Appendix 3.

***Juniperus scopulorum/Oryzopsis micrantha* Habitat Type**

This habitat type occurs on northwest to north-facing slopes of 35–70% and is recognized by the dominance of *J. scopulorum*; the vegetation is a topographic climax. Stands of this habitat type ordinarily cover entire hill-sides in TRNP, making them quite distinct even from a distance (fig. 13). Principal shrubs are *Prunus virginiana*, *Symphoricarpos occidentalis*, and *Rhus aromatica*; their abundance relates positively with openings among the dominant *Juniperus*. *Oryzopsis micrantha* dominates the undergrowth and is also characteristic of this habitat type. Mosses and lichens cover about 72% of the ground surface (table A8). In the seven stands of this habitat type sampled, 52 species occurred.

Major undergrowth species in stands of this habitat type and their constancy and mean coverage percentages are as follows:

Species	Constancy	Mean coverage
<i>Oryzopsis micrantha</i>	100	66.9
Mosses and Lichens	100	72.3
<i>Galium boreale</i>	100	4.5
<i>Rhus aromatica</i>	100	4.2
<i>Symphoricarpos occidentalis</i>	100	1.7
<i>Campanula rotundifolia</i>	100	1.0
<i>Prunus virginiana</i>	86	10.5

Mean coverages provided by all shrubs, graminoids, and forbs are the following:

shrubs:	mean coverage = 17.4%;	S.E. = 7.76
graminoids:	mean coverage = 69.1%;	S.E. = 3.72
forbs:	mean coverage = 9.4%;	S.E. = 1.77.

The mean forb coverage is calculated without the moss and lichen coverage. Shrubs are not as important in this association as in the other forest associations of TRNP. The undergrowth is dominated by herbaceous species primarily.

Fraxinus pennsylvanica is present in most of the stands; but most are seedlings which grow in slight depressions where soil moisture exceeds normal for this habitat type. There is no evidence at present to suggest that *Fraxinus* will replace *Juniperus scopulorum* as the climax dominant. The largest *Juniperus* sampled are in the 3–4-dm d.b.h. size class (appendix 2). Occasionally, larger ones are observed. Many of the trees have more than 125 xylem layers, and some have more than 250. Tree basal areas for the stands sampled ranged from 22.1 m²/ha to 29.6 m²/ha. Before TRNP was established, the primary use made of these stands was the harvest of *Juniperus* for use as fence posts (Ralston 1960). Limited cattle grazing occurred, although game species used the stands extensively. Deer still utilize stands of this habitat type quite extensively. There are numerous game trails over much of the area of this habitat type; *Achillea millefolium* is most abundant along these trails. The physiognomy of these stands is similar to that of the pinyon-juniper stands of the Southwest, although pine is absent. Edaphic characteristics are given in Appendix 3.

***Symphoricarpos occidentalis* Community**

This community occurs as scattered thickets over much of the study area. It is recognized by the dominance of *Symphoricarpos occidentalis* which forms dense thickets a few to several meters across (fig. 14). Observations suggest that these thickets may be long-lived seral communities (associates) occurring in at least two habitat types in TRNP. Typically, the community has three layers, an upper layer 0.5–1.0 m tall dominated by *Symphoricarpos occidentalis* and *Rosa woodsii*, an intermediate layer 0.2–1.5 m tall dominated by *Agropyron smithii*, *A. caninum*, *Lactuca oblongifolia*, and *Poa pratensis*, and a lower layer 0.1–0.3 m tall dominated by *Achillea millefolium*, *Artemisia ludoviciana*, and *Galium boreale*. In some of the larger, more complex thickets, there is a fourth taller layer dominated by *Prunus virginiana*, 2–3 m tall, with *Ribes odoratum* and *Rosa woodsii*. A total of 37 species occur in the five stands sampled. Most of the forbs grow near the margins of the thickets, where the shrubs are less dense. *Artemisia ludoviciana* and *Parietaria pennsylvanica* reach their maximum coverage and constancy in this community.

Symphoricarpos occidentalis thickets at TRNP occur on various exposures and substrates, from fine-textured alluvial soils of the *Artemisia cana/Agropyron smithii* habitat type to the coarse, gravelly substrates of the *Andropogon scoparius/Carex filifolia* habitat type. They also occur near margins of *Fraxinus*-dominated habitat types described above.

Symphoricarpos thickets also have been described in steppe vegetation elsewhere (Daubenmire 1970, Mackie 1970).



Figure 13a—Stand of *Juniperus scopulorum*/*Oryzopsis micrantha* habitat type on north-facing slope.



Figure 13b.—Interior of stand of *Juniperus*/*Oryzopsis* association showing the characteristically dense vegetation.



Figure 14.—Dense thicket of *Symphoricarpos occidentalis* with others in the background.

KEY TO THE HABITAT TYPES

1. Tree species absent
2. Herbaceous species dominant
 3. *Stipa Comata* well represented; *Agropyron smithii* and/or *Andropogon scoparius* inconspicuous or absent *Stipa comata*/*Carex filifolia* habitat type.
 3. *Agropyron smithii* and/or *Andropogon scoparius* dominant; *Stipa comata* inconspicuous or absent.
 4. *Agropyron smithii* abundant; *Andropogon scoparius* absent *Agropyron smithii*/*Carex filifolia* habitat type.
 4. *Andropogon scoparius* abundant *Andropogon scoparius*/*Carex filifolia* habitat type.
2. Shrub species dominant
 5. *Artemisia tridentata* or *A. cana* present and conspicuous.
 6. *Artemisia tridentata* dominant; *Artemisia cana* absent *Artemisia tridentata*/*Agropyron smithii* habitat type.
 6. *Artemisia cana* dominant; *Artemisia tridentata* absent *Artemisia cana*/*Agropyron smithii* habitat type.
 5. *Artemisia tridentata* and *A. cana* absent or inconspicuous.
 7. *Juniperus horizontalis* principal shrub; *Symphoricarpos occidentalis* if present is widely scattered and drawfed *Juniperus horizontalis*/*Andropogon scoparius* habitat type.
 7. *Symphoricarpos occidentalis* forming dense thickets or clones up to 1 m or more in height *Symphoricarpos occidentalis* community type.
1. Tree species present and dominant
 8. *Populus deltoides* and/or *Fraxinus pennsylvanica* dominant or exhibiting adequate reproduction to become dominant.
 9. Undergrowth dominated by *Prunus virginiana*... *Fraxinus pennsylvanica*/*Prunus virginiana* habitat type.
 9. Undergrowth dominated by *Symphoricarpos occidentalis*; *Prunus virginiana* absent or inconspicuous *Fraxinus pennsylvanica*/*Symphoricarpos occidentalis* habitat type.
 8. *Populus deltoides* and/or *Fraxinus pennsylvanica* absent or present in seedling and sapling size only.
 10. *Populus tremuloides* dominant; *Juniperus scopulorum* absent or rare *Populus tremuloides*/*Betula occidentalis* habitat type.
 10. *Juniperus scopulorum* dominant; *Populus tremuloides* absent *Juniperus scopulorum*/*Oryzopsis micrantha* habitat type.

DISCUSSION

Validation of the Habitat Type Classification

Natural vegetation is a convenient characteristic of the landscape to use in a classification scheme; the more mature the vegetation is, the more closely it reflects the biotic potential of the landscape (Daubenmire 1976).

A classification scheme provides a systematic ordering of the landscape units under study. In this case, the units are the habitat types, and the manner of delimiting these provides as natural a classification as possible. Because a habitat type consists of land units representing areas of similar environment, other research efforts can be related to the habitat types. For example, wildlife utilization (Mackie 1970), small mammal distributions (Hoffman 1960, Rickard 1957), growth rates of ponderosa pine (Daubenmire 1961), depth of soil moisture drying (Daubenmire 1972), and productivity and grazing potentials (Bjugstad and Whitman 1970, Mueggler and Stewart 1980), can be related to the habitat types to provide a means of correlating and communicating research results. Silvicultural and watershed management implications also have been discussed in relation to habitat types (Hoffman and Alexander 1976, 1980, 1983).

Species Diversity

Species diversity may be described as the median number of species occurring in areas of constant sam-

pling size (Daubenmire 1970). Species diversity of the habitat types encountered in this study is shown in table 2. Among the steppe habitat types, diversity ranged from a low of 10 in the *Agropyron smithii*/*Carex filifolia* habitat type to a high of 29 in the *Juniperus horizontalis*/*Andropogon scoparius* habitat type. Four of the five stands sampled of the *Juniperus*/*Andropogon* habitat type are on north-facing slopes, with reduced solar insolation. This may be an important factor in influencing species diversity in the semi-arid climate of western North Dakota. Among the edaphic characteristics measured, surface soils of this habitat type are similar to those of the *Andropogon scoparius*/*Carex filifolia* and *Agropyron smithii*/*Carex filifolia* habitat types, the latter of which had the lowest median species diversity. The low species diversity of the *Agropyron*/*Carex* habitat type is possibly related to the very high coverage of *Agropyron* (table A2). Shantz (1924) described dense, almost pure stands of *Agropyron smithii*, accompanied by a paucity of forbs in west-central South Dakota. Possibly the density of the *Agropyron* sod inhibits the successful establishment of numerous other species.

Species diversity among habitat types dominated by tree species ranged from 21 in the *Juniperus scopulorum*/*Oryzopsis micrantha* habitat type to 30 in the *Populus tremuloides*/*Betula occidentalis* habitat type, which included six tree species. The remaining two habitat types dominated by trees had 29 species each. The generally higher numbers of species in the tree-dominated habitat types probably reflects the wetter conditions compared to the steppe vegetation of TRNP.

Table 2.—Species diversity in habitat types of Theodore Roosevelt National Park

Habitat type	No. of stands studied	Median no. of shrub, graminoid, and forb species per H.T. ¹	Total tree species per H.T. ²
<i>Stipa comata</i> / <i>Carex filifolia</i>	7	23	
<i>Agropyron smithii</i> / <i>Carex filifolia</i>	9	10	
<i>Andropogon scoparius</i> / <i>Carex filifolia</i>	9	22	
<i>Juniperus horizontalis</i> / <i>Andropogon scoparius</i>	5	29	
<i>Artemisia tridentata</i> / <i>Agropyron smithii</i>	4	14	
<i>Artemisia cana</i> / <i>Agropyron smithii</i>	12	13	
<i>Fraxinus pennsylvanica</i> / <i>Symphoricarpos occidentalis</i>	4	26	3
<i>Fraxinus pennsylvanica</i> / <i>Prunus virginiana</i>	4	25	4
<i>Populus tremuloides</i> / <i>Betula occidentalis</i>	4	24	6
<i>Juniperus scopulorum</i> / <i>Oryzopsis micrantha</i>	7	19	2
<i>Symphoricarpos occidentalis</i> community type	5	15	

¹Based on fifty 0.1 m² microplots, per stand.

²Based on 375 m² per stand.

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APPENDIX 1. HABITAT TYPE TABLES WITH STAND DATA

In the plant data, the number to the left of the dot is percent coverage where the value exceeds 0.5%, with a + to the left of dot indicating coverage of 0.5% or less. Number to the right of dot is percent frequency. Species present in the macroplot but not in the microplots are indicated by an asterisk (*). Stand numbers, locations, and topographic positions are also given.

Table A1.—*Stipa comata*/*Carex filifolia* habitat type

	Stand number						
	27	35	36	39	40	56	61
Location							
Quarter section	NW	SW	SE	NW	NE	SW	NW
Section	16	2	3	11	11	24	32
Township	140N	140N	140N	140N	140N	148N	148N
Range	102W	101W	101W	101W	101W	100W	100W
Topographic position							
Slope (%)	0	0	0	4	8	18	3
Aspect (°)	0	0	0	270	292	178	269
Elevation (m)	823	823	835	823	826	750	774
Coverage/Frequency							
SHRUBS							
<i>Artemisia cana</i>	.	.	+ .2
<i>Artemisia frigida</i>	1.4	4.52	3.34	1.12	3.40	5.60	6.60
<i>Yucca glauca</i>	+ .2	.	.
GRAMINOIDS							
<i>Agropyron caninum</i>	.	.	.	+ .2	.	.	+ .6
<i>Agropyron smithii</i>	68.98	1.12	+ .8	1.18	2.6	.	.
<i>Andropogon scoparius</i>	.	1.4
<i>Aristida longiseta</i>	+ .2
<i>Bouteloua gracilis</i>	.	1.20	2.24	+ .2	2.18	+ .8	1.6
<i>Bromus tectorum</i>	.	.	1.4
<i>Calamovilfa longifolia</i>	.	.	.	+ .2	.	1.4	.
<i>Carex eleocharis</i>	4.26	1.22	1.28	2.28	1.14	+ .8	+ .6
<i>Carex filifolia</i>	48.99	24.84	37.98	15.80	22.76	49.99	4.36
<i>Koeleria pyramidata</i>	3.28	10.72	13.84	5.58	14.66	8.38	15.94
<i>Poa interior</i>	.	+ .8	+ .8	.	.	.	+ .2
<i>Stipa comata</i>	11.64	41.94	52.99	65.99	35.88	35.98	35.98
FORBS							
<i>Artemisia campestris</i>	.	+ .2	+ .6
<i>Artemisia dracunculus</i>	5.22	4.34	1.28	+ .4	5.42	3.32	1.6
<i>Aster oblongifolius</i>	+ .2	.
<i>Astragalus crassicaulis</i>	.	.	.	+ .2	.	.	.
<i>Astragalus lotiflorus</i>	.	.	+ .2
<i>Chenopodium album</i>	.	.	+ .2
<i>Coryphantha vivipara</i>	+ .2	.	.
<i>Chrysopsis villosa</i>	.	6.32	1.14	2.4	2.24	.	14.64
<i>Echinacea angustifolia</i>	+ .2
<i>Eriogonum flavum</i>	+ .2
<i>Erysimum asperum</i>	.	+ .2	+ .2
<i>Gaura coccinea</i>	2.26	+ .2	.	1.4	1.6	1.6	+ .8
<i>Gentianella amarella</i>	+ .2
<i>Helianthus rigidus</i>	1.6	.
<i>Lactuca oblongifolia</i>	1.20	6.78	3.42	2.44	8.82	8.76	.
<i>Liatris punctata</i>	.	+ .8	+ .10	+ .8	.	+ .2	1.12
<i>Linum perenne</i>	.	.	.	+ .8	.	.	.
<i>Linum rigidum</i>	+ .8	.
<i>Lithospermum incisum</i>	.	1.36	1.36	1.40	1.30	+ .2	.
<i>Lygodesmia juncea</i>	.	2.40	1.40	+ .18	1.32	2.24	.
<i>Melilotus officinalis</i>	.	+ .4
<i>Opuntia polyacantha</i>	.	+ .2	.	1.14	+ .2	+ .2	.
<i>Oxytropis lambertii</i>	1.10	+ .2	7.70
<i>Petalostemon purpureum</i>	.	.	+ .2	.	.	.	+ .6
<i>Polygala alba</i>	+ .6	+ .2
<i>Potentilla pensylvanica</i>	.	+ .2	.	.	+ .4	+ .4	.
<i>Psoralea argophylla</i>	4.44	+ .6	.	+ .2	+ .18	+ .8	.
<i>Ratibida columnifera</i>	1.8	+ .2	.	.	.	+ .2	.
<i>Selaginella densa</i>	39.92	43.92	43.99	54.90	42.88	28.96	84.99
<i>Sphaeralcea coccinea</i>	+ .2
<i>Thermopsis rhombifolia</i>	+ .4	.	.
<i>Tragopogon dubius</i>	+ .12	+ .6	+ .4	+ .8	+ .8	1.10	+ .2
<i>Vicia americana</i>	.	.	.	+ .16	.	.	.
<i>Zigadenus venenosus</i>	.	+ .8	+ .8	+ .8	+ .6	+ .6	+ .2
Species in microplots	16	27	23	24	22	24	22
Coverage of shrubs	1	4	3	1	3	5	6
Coverage of graminoids	134	79	106	88	76	96	55
Coverage of forbs	53	62	50	61	60	44	107
Total coverage	188	145	159	150	139	145	168

Table A2.—*Agropyron smithii*/*Carex filifolia* habitat type

	Stand number								
	3	5	14	18	20	21	43	54	62
Location									
Quarter section	SE	SE	SE	SE	SE	NW	NW	NE	NE
Section	1	1	12	28	28	34	33	26	32
Township	140N	140N	140N	141N	141N	141N	148N	148N	148N
Range	102W	102W	102W	101W	101W	101W	99W	100W	99W
Topographic position									
Slope (%)	16	19	16	18	18	20	14	9	14
Aspect (°)	203	202	43	233	137	211	163	357	124
Elevation (m)	701	719	707	732	713	719	631	750	643
Coverage/Frequency									
SHRUBS									
<i>Artemisia cana</i>	+.4	.	.
<i>Artemisia frigida</i>	+.4	+.6	.	2.20	.	3.26	1.10	3.18	1.4
<i>Atriplex nuttallii</i>	+.2
<i>Ceratoides lanata</i>	+.4	2.6	.	.	1.4
GRAMINOIDS									
<i>Agropyron smithii</i>	93.99	92.99	98.99	86.99	91.99	82.99	93.99	96.99	91.99
<i>Aristida longiseta</i>	1.4	.	.	.
<i>Bouteloua gracilis</i>	10.42	2.24	.	16.36
<i>Carex eleocharis</i>	1.4	.
<i>Carex filifolia</i>	28.62	.	.	27.72	29.84	17.64	1.4	24.94	+.2
<i>Koeleria pyramidata</i>	.	.	.	+.2	.	.	.	3.30	+.2
<i>Stipa comata</i>	.	.	.	3.16	4.34	2.16	1.20	+.2	+.2
<i>Stipa viridula</i>	3.12	4.14	.	3.14	4.22
FORBS									
<i>Achillea millefolium</i>	+.8	.
<i>Arabis holboellii</i>	+.4	.	.	.
<i>Artemisia dracunculus</i>	+.2	.
<i>Conyza canadensis</i>	6.44	.	.
<i>Coryphantha vivipara</i>	+.2	+.2	.	.
<i>Euphorbia podperae</i>	+.2
<i>Gaura coccinea</i>	+.6	.	.
<i>Hedeoma hispida</i>	+.2
<i>Lactuca oblongifolia</i>	1.10	+.8	.	1.22	.	.	1.4	+.4	.
<i>Linum perenne</i>	.	.	+.2	+.2
<i>Melilotus officinalis</i>	+.6
Mosses & Lichens	2.28	+.2	.	+.2	.	.	.	1.4	.
<i>Opuntia polyacantha</i>	+.2	.	.
<i>Plantago patagonica</i>	2.32	.	.
<i>Polygala alba</i>	1.14	2.14	.	.	.
<i>Ratibida columnifera</i>	1.12	1.16	.	+.10	.
<i>Selaginella densa</i>	+.6
<i>Senecio plattensis</i>	+.4	+.4	.	.	.
<i>Sphaeralcea coccinea</i>	+.6	2.34	.	.	.	+.6	.	.	.
<i>Taraxacum officinale</i>	+.2
<i>Tragopogon dubius</i>	.	+.8	.	+.2	+.4	+.6	+.2	+.2	+.4
Species in microplots ¹	12	8	2	10	9	12	13	12	10
Coverage of shrubs	0	2	0	2	1	3	1	3	1
Coverage of graminoids	124	96	98	119	124	112	97	124	111
Coverage of forbs	3	2	0	1	2	3	9	1	0
Total coverage	127	100	98	122	127	118	107	128	112

¹Mosses and lichens are counted as one species in the total list.

Table A3.—*Andropogon scoparius*/*Carex filifolia* habitat type

	Stand number								
	8	15	22	23	24	46	55	63	64
Location									
Quarter section	SE	NE	SE	SE	NW	SE	NE	NE	NE
Section	28	13	35	35	4	29	26	28	28
Township	141N	140N	141N	141N	140N	147N	148N	148N	148N
Range	101W	102W	101W	101W	101W	100W	100W	100W	100W
Topographic position									
Slope (%)	27	18	28	30	42	13	6	16	0
Aspect (°)	271	242	70	205	195	300	193	179	0
Elevation (m)	738	738	747	747	747	725	744	716	719
Coverage/Frequency									
SHRUBS									
<i>Artemisia cana</i>				3.14					
<i>Artemisia frigida</i>	+ 8	2.28	+ 2	+ 4	+ 4	+ 2	+ 2		+ 10
<i>Ceratoides lanata</i>					+ 2				
<i>Gutierrezia sarothrae</i>			+ 2						
<i>Juniperus horizontalis</i>	1.4					+ 2			
<i>Rhus aromatica</i>			1.4						
<i>Rosa arkansana</i>	+ 10	+ 2	+ 6			1.16			+ 6
<i>Shepherdia argentea</i>									+ 2
<i>Symphoricarpos occidentalis</i>			3.2						
<i>Yucca glauca</i>		+ 2					+ 12		
GRAMINOIDS									
<i>Agropyron smithii</i>			+ 4	+ 8			+ 2		
<i>Andropogon scoparius</i>	68.99	88.99	88.99	72.98	65.99	84.99	70.98	77.99	81.99
<i>Bouteloua curtipendula</i>			3.16	14.44	19.80		+ 2	3.12	
<i>Bouteloua gracilis</i>					1.10		+ 4	+ 2	
<i>Calamovilfa longifolia</i>	6.30	+ 4	4.32	14.42	8.34	+ 2	14.74	+ 4	1.12
<i>Carex filifolia</i>	8.40	9.58	2.18	13.54	9.48	12.56	10.52	8.60	10.72
<i>Carex sprengei</i>	4.44								
<i>Koeleria pyramidata</i>	+ 2	+ 8	1.18		+ 2	1.10	2.22	1.10	1.14
<i>Muhlenbergia cuspidata</i>						+ 2	1.8		
<i>Stipa comata</i>	+ 2		+ 2	3.18	1.6			+ 4	
FORBS									
<i>Agoseris glauca</i>			+ 2						
<i>Anemone cylindrica</i>						+ 6			+ 2
<i>Anemone patens</i>	1.18	+ 4							
<i>Antennaria parviflora</i>	+ 4	1.20	+ 2						
<i>Antennaria rosea</i>	+ 4					+ 2			
<i>Arabis holboellii</i>		+ 2							+ 2
<i>Artemisia dracunculoides</i>		+ 4							
<i>Aster laevis</i>						+ 4			
<i>Aster oblongifolius</i>	1.26	1.8	+ 4		+ 4	+ 8	+ 8	+ 12	+ 6
<i>Astragalus adsurgens</i>			+ 10						
<i>Astragalus crassicaulis</i>		+ 2							
<i>Astragalus gilviflorus</i>						+ 4			
<i>Calyptophorus serrulatus</i>	+ 4	+ 2	+ 2						
<i>Campanula rotundifolia</i>	+ 6	+ 2	+ 2			+ 2			
<i>Castilleja sessiliflora</i>			+ 2						
<i>Chrysopsis villosa</i>		+ 2							
<i>Cirsium undulatum</i>					1.4				
<i>Echinacea angustifolia</i>	2.34	+ 6	1.12		+ 8	+ 8	+ 14	1.26	+ 12
<i>Erigeron strigosus</i>			+ 2			+ 10	+ 2		
<i>Galium boreale</i>			+ 2						
<i>Gaura coccinea</i>	1.14	+ 4	+ 2	+ 4			2.36	1.22	
<i>Glycyrrhiza lepidota</i>								1.14	
<i>Hedeoma pinnatifida</i>					1.10				
<i>Helianthus rigidus</i>	3.20	+ 4	7.52			7.66	7.86	2.56	6.70
<i>Lactuca oblongifolia</i>	2.26	+ 12		2.36	4.58	1.30		+ 2	
<i>Liatris punctata</i>						+ 2			
<i>Linum perenne</i>	+ 6	+ 2	+ 6						
<i>Linum rigidum</i>					+ 2				
<i>Lithospermum incisum</i>									+ 2
<i>Lygodesmia juncea</i>	+ 10		+ 2		+ 8	+ 4	+ 8		1.4
<i>Medicago sativa</i>									+ 2
<i>Melilotus officinalis</i>						+ 2			1.16
Mosses & Lichens	2.38								
<i>Opuntia fragilis</i>				+ 2					
<i>Opuntia polyacantha</i>		+ 4	+ 4						
<i>Oxytropis lambertii</i>					+ 4				
<i>Petalostemon purpureum</i>	+ 6		+ 2				+ 4	+ 4	+ 2
<i>Polygala alba</i>	+ 4		+ 4	+ 2		+ 2	+ 4		+ 2
<i>Potentilla arguta</i>			+ 4	+ 2					
<i>Psoralea argophylla</i>				2.16	2.34		1.48		+ 8
<i>Psoralea esculenta</i>		+ 2					+ 2	+ 2	
<i>Senecio platensis</i>	+ 16	+ 6		1.10	+ 2	+ 2			
<i>Solidago rigida</i>	1.12		1.10						
<i>Sphaeralcea coccinea</i>			+ 8	+ 4	1.10				
<i>Tragopogon dubius</i>		+ 2			+ 2				
<i>Vicia americana</i>								+ 8	1.4
Species in microplots	26	25	32	15	22	23	20	16	20
Coverage of shrubs	1	2	4	3	0	1	0	0	0
Coverage of graminoids	86	97	98	116	103	97	97	89	94
Coverage of forbs	13	2	9	5	9	8	10	5	9
Total coverage	100	101	111	124	112	106	107	94	103

Table A4.—*Juniperus horizontalis*/*Andropogon scoparius* habitat type

	Stand number				
	9	10	12	44	47
Location					
Quarter section	NE	SE	SW	NW	SE
Section	1	15	12	22	33
Township	140N	140N	140N	140N	148N
Range	102W	102W	102W	101W	99W
Topographic position					
Slope (%)	28	48	30	46	32
Aspect (°)	349	268	9	21	338
Elevation (m)	719	725	719	753	628
Coverage/Frequency					
SHRUBS					
<i>Artemisia cana</i>		3.4			
<i>Artemisia frigida</i>			+ 2		
<i>Juniperus communis</i>	+ 8			2.2	
<i>Juniperus horizontalis</i>	61.92	82.99	85.99	85.98	90.99
<i>Potentilla fruticosa</i>	1.2	7.12	3.16	1.10	
<i>Prunus virginiana</i>		2.8			
<i>Rhus aromatica</i>	+ 4	7.16	1.2		
<i>Rosa arkansana</i>	+ 2	+ 8	+ 2		
<i>Shepherdia argentea</i>		1.2			
<i>Symphoricarpos occidentalis</i>		7.60	2.36	+ 4	
GRAMINOIDS					
<i>Agropyron caninum</i>				+ 4	+ 2
<i>Andropogon scoparius</i>	36.92	25.80	24.84	35.84	2.6
<i>Aristida longiseta</i>				+ 2	
<i>Bouteloua curtipendula</i>				+ 4	
<i>Calamovilfa longifolia</i>	8.54	4.32	15.48	8.36	2.12
<i>Carex filifolia</i>	1.16	1.12	5.20	5.36	3.30
<i>Carex sprengei</i>	+ 6	1.16			
<i>Koeleria pyramidata</i>	1.4	+ 6	+ 4	+ 4	1.4
<i>Muhlenbergia cuspidata</i>				3.12	
<i>Stipa spartea</i>				1.10	31.88
FORBS					
<i>Achillea millefolium</i>		+ 12	+ 2		
<i>Anemone cylindrica</i>				1.42	
<i>Anemone patens</i>	4.54	3.24	3.50		2.52
<i>Antennaria parviflora</i>	+ 2		+ 2		
<i>Antennaria rosea</i>				+ 2	+ 2
<i>Artemisia campestris</i>	+ 6				
<i>Aster falcatus</i>		2.12			
<i>Aster laevis</i>	+ 2			+ 16	2.28
<i>Aster oblongifolius</i>	1.12		+ 2		+ 4
<i>Astragalus adsurgens</i>	+ 2				
<i>Astragalus gilviflorus</i>	+ 6	1.14	2.26		
<i>Astragalus</i> sp.			1.4		
<i>Campanula rotundifolia</i>	2.18	1.14	1.12	+ 14	2.32
<i>Chenopodium album</i>				+ 2	
<i>Echinacea angustifolia</i>	+ 14	1.14	1.18		+ 2
<i>Erigeron strigosus</i>					+ 8
<i>Eriogonum flavum</i>	+ 4				
<i>Galium boreale</i>		9.66	6.76	3.72	6.82
<i>Gaura coccinea</i>	1.6	1.10	+ 14		1.22
<i>Geum triflorum</i>					+ 2
<i>Hedysarum boreale</i>	12.40				
<i>Helianthus rigidus</i>	2.24	+ 4	+ 8		
<i>Liatris punctata</i>	+ 10	+ 2			
<i>Linum perenne</i>	+ 8	+ 8		+ 4	+ 6
<i>Linum rigidum</i>	+ 2				
<i>Lygodesmia juncea</i>	1.10		+ 8		
<i>Melilotus albus</i>					+ 2
<i>Melilotus officinalis</i>				1.4	4.26
Mosses & Lichens	+ 4	1.10	1.10		
<i>Opuntia polyacantha</i>				+ 2	
<i>Oxytropis lambertii</i>	+ 4			+ 2	+ 8
<i>Petalostemon purpureum</i>	1.18	+ 2	+ 14	1.12	1.22
<i>Polygala alba</i>	+ 4		+ 2		
<i>Potentilla pensylvanica</i>			1.2		
<i>Psoralea esculenta</i>	+ 4		+ 2		
<i>Senecio plattensis</i>	+ 8	+ 6	+ 4	1.10	
<i>Solidago nemoralis</i>	+ 8				
<i>Solidago rigida</i>	+ 2				
<i>Thermopsis rhombifolia</i>	1.18	+ 2			
<i>Vicia americana</i>		2.22	+ 6		
<i>Viola</i> sp.					+ 2
Species in microplots	36	29	29	25	23
Coverage of shrubs	62	109	91	88	90
Coverage of graminoids	46	31	44	52	39
Coverage of forbs	25	21	16	7	18
Total coverage	133	161	151	147	147

Table A5.—*Artemisia tridentata*/*Agropyron smithii* habitat type

	Stand number			
	4	13	16	28
Location				
Quarter section	SE	SW	SW	NW
Section	1	12	20	4
Township	140N	140N	140N	140N
Range	102W	102W	101W	101W
Topographic position				
Slope (%)	49	5	10	22
Aspect (°)	77	185	97	45
Elevation (m)	725	732	783	765
Coverage/Frequency				
SHRUBS				
<i>Artemisia frigida</i>	.	.	+ .2	+ .2
<i>Artemisia tridentata</i>	17.56	36.88	27.72	41.82
<i>Atriplex confertifolia</i>	4.14	.	2.2	+ .2
<i>Atriplex nuttallii</i>	.	+ .2	.	.
<i>Ceratoides lanata</i>	+ .2	.	2.4	+ .2
<i>Eriogonum pauciflorum</i>	.	.	.	+ .2
<i>Gutierrezia sarothrae</i>	.	1.8	.	+ .2
<i>Ribes setosum</i>	.	.	+ .4	.
<i>Symphoricarpos occidentalis</i>	.	.	4.16	.
GRAMINOIDS				
<i>Agropyron caninum</i>	7.28	20.50	4.16	2.6
<i>Agropyron smithii</i>	64.99	45.90	86.98	81.99
<i>Andropogon scoparius</i>	+ .2	.	.	.
<i>Bouteloua gracilis</i>	.	.	.	+ .2
<i>Carex filifolia</i>	.	.	1.16	12.90
<i>Muhlenbergia cuspidata</i>	.	.	3.24	+ .2
<i>Koeleria pyramidata</i>	.	.	.	3.6
<i>Stipa viridula</i>	.	.	1.4	3.14
FORBS				
<i>Achillea millefolium</i>	.	.	4.18	1.6
<i>Astragalus agrestis</i>	1.8	+ .6	.	.
<i>Gaura coccinea</i>	.	.	.	+ .2
<i>Geum triflorum</i>	.	+ .4	.	.
<i>Lactuca oblongifolia</i>	+ .6	.	2.30	+ .4
Mosses & Lichens	+ .2	.	.	.
<i>Opuntia polyacantha</i>	+ .2	+ .4	+ .4	1.8
<i>Parietaria pennsylvanica</i>	.	.	2.10	.
<i>Polygala alba</i>	.	.	.	1.4
<i>Ratibida columnifera</i>	.	.	.	1.14
<i>Sphaeralcea coccinea</i>	+ .2	+ .2	.	.
<i>Vicia americana</i>	1.14	+ .4	+ .2	.
Summary				
Species in microplots	12	10	16	19
Coverage of shrubs	21	37	35	41
Coverage of graminoids	71	65	95	101
Coverage of forbs	2	0	8	4
Total coverage	94	102	138	146

Table A6.—*Artemisia cana*/*Agropyron smithii* habitat type

	Stand number											
	1	6	7	26	66	69	70	2	25	31	32	65
Location												
Quarter section	SE	NW	NW	SE	NW	NW	NW	SE	NW	NE	SE	SW
Section	1	6	6	35	30	30	30	1	4	14	1	33
Township	140N	140N	140N	140N	148N	148N	148N	140N	140N	140N	140N	148N
Range	102W	101W	101W	101W	99W	99W	99W	102W	101W	102W	102W	99W
Topographic position												
Slope (%)	0	5	5	5	0	0	4	0	8	7	0	0
Aspect (°)	0	245	287	32	0	0	76	0	293	245	0	0
Elevation (m)	683	707	706	744	613	619	619	683	744	683	689	600
Coverage/Frequency												
SHRUBS												
<i>Artemisia cana</i>	24.80	48.88	26.70	36.74	34.62	26.50	42.80	32.64	45.82	18.48	51.96	21.66
<i>Artemisia frigida</i>		+ 2	+ 2	+ 4					3.6	+ 6	1.8	3.16
<i>Ceratoides lanata</i>		4.14	1.2	+ 4					2.8			
<i>Gutierrezia sarothrae</i>					+ 2							+ 2
<i>Rosa woodsii</i>												1.2
<i>Symphoricarpos occidentalis</i>								63.82	24.48	61.72	13.26	70.88
GRAMINOIDS												
<i>Agropyron caninum</i>		+ 4	2.10	4.10				7.20	3.8	23.72	13.32	27.54
<i>Agropyron smithii</i>	79.99	80.99	88.99	73.94	95.99	96.99	97.99	31.52	84.99	25.42	57.93	46.76
<i>Bouteloua gracilis</i>							+ 8					
<i>Bromus inermis</i>											1.2	
<i>Calamagrostis inexpansa</i>						+ 2	1.6					
<i>Calamovilfa longifolia</i>				5.10						2.4		
<i>Carex filifolia</i>				+ 4					+ 2			
<i>Distichlis spicata</i>						+ 2			5.10			
<i>Muhlenbergia cuspidata</i>				5.12								
<i>Muhlenbergia racemosa</i>										+ 2		
<i>Poa arida</i>				+ 6								7.26
<i>Poa interior</i>	9.44	1.4		2.6				1.6				
<i>Poa palustris</i>				1.8				1.4	4.18			
<i>Poa pratensis</i>										13.32		2.4
<i>Stipa comata</i>				1.4								
<i>Stipa viridula</i>		2.12	+ 4	11.30		3.16	2.12		1.6	1.8	+ 4	8.28
FORBS												
<i>Achillea millefolium</i>	7.36	3.14		+ 4	1.2				1.2	2.16		4.32
<i>Artemisia dracunculus</i>												+ 2
<i>Artemisia ludoviciana</i>		2.6								6.18		
<i>Aster oblongifolius</i>										+ 4		
<i>Astragalus agrestis</i>									1.8			
<i>Chenopodium album</i>								+ 8				
<i>Convolvulus sepium</i>											+ 2	
<i>Coryza canadensis</i>							1.12				3.28	
<i>Erigeron strigosus</i>							+ 4					
<i>Euphorbia podperae</i>		+ 6										
<i>Euphorbia spathulata</i>									+ 2			
<i>Galium aparine</i>		+ 4						1.8				
<i>Gaura coccinea</i>				2.14					1.6	1.4	+ 8	
<i>Grindelia squarrosa</i>					+ 2							
<i>Hedeoma hispida</i>								+ 2	+ 2			
<i>Helianthus rigidus</i>									+ 2			
<i>Lactuca oblongifolia</i>				11.38	+ 2			1.16	10.54			
<i>Linum perenne</i>				+ 4					2.12			
<i>Melilotus officinalis</i>				+ 6	1.10	+ 2				+ 2	3.24	
<i>Monarda fistulosa</i>									+ 2			
Mosses & Lichens	11.70							+ 4				
<i>Opuntia fragilis</i>											+ 2	
<i>Opuntia polyacantha</i>		+ 2										
<i>Parietaria pennsylvanica</i>		15.44	1.6					3.48	+ 6		2.12	
<i>Plantago patagonica</i>											+ 4	
<i>Psoralea esculenta</i>				6.24								
<i>Ratibida columnifera</i>				+ 2			1.4		+ 6			
<i>Solidago missouriensis</i>											2.4	
<i>Solidago rigida</i>									1.2			
<i>Sphaeralcea coccinea</i>		1.10	+ 2							+ 2		
<i>Taraxacum officinale</i>							+ 4					
<i>Thalictrum dasycarpum</i>										1.4		
<i>Tragopogon dubius</i>							+ 2					
<i>Vicia americana</i>		1.4			1.10			1.12	1.10	+ 2	1.12	
Species in microplots	5	14	8	20	8	6	10	13	23	18	16	12
Coverage of shrubs	24	52	27	36	34	26	42	95	74	79	65	95
Coverage of graminoids	88	83	90	102	95	99	100	40	97	63	71	90
Coverage of forbs	18	22	1	19	3	0	2	6	17	10	11	4
Total coverage	130	157	118	157	132	125	144	141	188	152	147	189

Table A7.—*Fraxinus pennsylvanica*/*Symphoricarpos occidentalis*, *Fraxinus pennsylvanica*/*Prunus virginiana*, and *Populus tremuloides*/*Betula occidentalis* habitat types

	Stand number											
	<i>Fraxinus</i> / <i>Symphoricarpos</i> H.T.				<i>Fraxinus</i> / <i>Prunus</i> H.T.				<i>Populus</i> / <i>Betula</i> H.T.			
	29	30	51	52	41	42	57	58	43	60	67	68
Location												
Quarter section	SE	SE	NW	SW	SW	SW	SE	NW	SW	NE	NW	SE
Section	16	16	31	31	11	11	21	27	35	32	11	3
Township	140N	140N	148N	148N	140N	140N	148N	148N	140N	148N	147N	147N
Range	102W	102W	99W	99W	102W	102W	100W	100W	101W	100W	100W	100W
Topographic position												
Slope (%)	0	11	2	0	0	3	6	14	77	13	23	48
Aspect (°)	0	28	24	0	0	283	340	25	30	73	341	320
Elevation (m)	683	683	600	600	710	707	732	728	838	753	765	759
Coverage/Frequency												
SHRUBS												
<i>Amelanchier alnifolia</i>	4.4	.	.
<i>Arctostaphylos uva-ursi</i>
<i>Betula occidentalis</i>	7.30	1.6	32.68	49.74
<i>Celastrus scandens</i>	+ 2	1.8	+ 2	+ 2
<i>Clematis ligusticifolia</i>	+ 4	.	1.4	2.12	+ 2	1.10	.	+ 2	.	.	.	+ 4
<i>Cornus stolonifera</i>	.	.	+ 2	1.2	+ 2	.	2.4
<i>Juniperus communis</i>	1.12	+ 6	1.20	.	.	+ 2
<i>Juniperus horizontalis</i>
<i>Parthenocissus vitacea</i>	+ 4	+ 2	2.10	1.2
<i>Potentilla fruticosa</i>
<i>Prunus virginiana</i>	17.40	44.76	19.32	31.70	36.76	37.70	35.80	16.50
<i>Rhus aromatica</i>	11.32	3.8	1.2	8.18	+ 2	3.4	.	.	+ 2	.	.	.
<i>Ribes odoratum</i>	+ 2	+ 2	.	+ 2
<i>Ribes setosum</i>	1.12	1.2	3.16	+ 4	+ 2	1.10	1.2	+ 2
<i>Rosa woodsii</i>	1.8	2.10	9.56	13.50	2.8	16.50	.	.	+ 6	+ 6	3.22	.
<i>Rubus idaeus</i>	4.14	.	.
<i>Salix bebbiana</i>
<i>Shepherdia argentea</i>	+ 2	1.4	9.28	.	.	.
<i>Symphoricarpos albus</i>	31.86	10.40
<i>Symphoricarpos occidentalis</i>	22.90	14.50	45.94	81.99	18.76	23.84	1.4	7.36	21.80	6.46	.	.
<i>Toxicodendron rydbergii</i>	17.62	2.14	61.99	12.28	+ 2	.	.	.	30.82	6.46	21.76	+ 4
<i>Vitis vulpina</i>	+ 2
GRAMINOIDS												
<i>Agropyron caninum</i>	9.36	5.24	1.6	2.8	.	.	1.6	.	.	.	2.10	.
<i>Bromus inermis</i>
<i>Calamovilfa longifolia</i>	16.36	29.64
<i>Carex sprengei</i>	.	+ 2	52.88	70.92	.	25.44	9.18	.
<i>Elymus canadensis</i>	12.38	25.66	7.22	2.12	+ 2	.	.	.
<i>Elymus villosus</i>	29.66
<i>Elymus virginicus</i>	38.96	41.90	30.90	1.2	1.6	.	.	.
<i>Muhlenbergia racemosa</i>	8.4	5.22	15.64	5.14	.	.	.	1.6	.	+ 2	.	.
<i>Oryzopsis micrantha</i>	.	.	.	2.6	.	.	+ 2	.	36.86	10.30	.	.
<i>Poa paulstris</i>	1.6
<i>Poa pratensis</i>	60.90	51.94	1.6	.	6.10	17.26	39.60	.	+ 2	.	.	.
<i>Schizachne purpurascens</i>	3.10
<i>Scirpus americanus</i>	.	.	1.4
<i>Stipa viridula</i>	.	1.4	+ 2
FORBS												
<i>Achillea millefolium</i>	+ 6	.	1.12	+ 2	.	.
<i>Ambrosia psilostachya</i>	.	1.10	2.12
<i>Anemone cylindrica</i>	.	.	+ 2	1.2	+ 6	.	.	.
<i>Antennaria plantaginifolia</i>	.	1.8
<i>Apocynum androsaemifolium</i>
<i>Apocynum cannabinum</i>	33.72	12.42	1.4
<i>Aralia nudicaulis</i>	4.22	.	.
<i>Arctium minus</i>	9.64	1.14	+ 2	.	.	.	20.64	.

Table A7.—*Fraxinus pennsylvanica*/*Symphoricarpos occidentalis*, *Fraxinus pennsylvanica*/*Prunus virginiana*, and *Populus tremuloides*/*Betula occidentalis* habitat types—Continued

	Stand number											
	<i>Fraxinus</i> / <i>Symphoricarpos</i> H.T.				<i>Fraxinus</i> / <i>Prunus</i> H.T.				<i>Populus</i> / <i>Betula</i> H.T.			
	29	30	51	52	41	42	57	58	43	60	67	68
Location												
Quarter section	SE	SE	NW	SW	SW	SW	SE	NW	SW	NE	NW	SE
Section	16	16	31	31	11	11	21	27	35	32	11	3
Township	140N	140N	148N	148N	140N	140N	148N	148N	140N	148N	147N	147N
Range	102W	102W	99W	99W	102W	102W	100W	100W	101W	100W	100W	100W
Topographic position												
Slope (%)	0	11	2	0	0	3	6	14	77	13	23	48
Aspect (°)	0	28	24	0	0	283	340	25	30	73	341	320
Elevation (m)	683	683	600	600	710	707	732	728	838	753	765	759
Coverage/Frequency												
<i>Artemisia ludoviciana</i>	+ .4	.	1.6
<i>Asclepias verticillata</i>
<i>Asparagus officinalis</i>
<i>Aster laevis</i>	+ .2	+ .8	+ .2	.	.	.
<i>Astragalus agrestis</i>	+ .4	.	.	.
<i>Campanula rotundifolia</i>	+ .4	.	+ .2	.
<i>Chenopodium album</i>	+ .6	+ .6
<i>Convolvulus arvensis</i>	+ .4
<i>Convolvulus sepium</i>	+ .4
<i>Disporum trachycarpum</i>	1.4	2.26	+ .2	4.32	15.86
<i>Euphorbia podperae</i>	+ .2
<i>Fragaria virginiana</i>	3.40	1.10	.	4.60	1.16
<i>Galium aparine</i>	1.4
<i>Galium boreale</i>	4.10	.	.	4.28	19.74	3.14	12.76	7.56	5.34	8.46	7.38	+ .2
<i>Geranium carolinianum</i>	1.4	.	.
<i>Glycyrrhiza lepidota</i>	.	.	2.10
<i>Hackelia deflexa</i>	+ .2
<i>Helianthus rigidus</i>	.	.	+ .4
<i>Heuchera richardsonii</i>	1.8	1.14	+ .2	.	.
<i>Lactuca oblongifolia</i>	.	.	1.12	+ .4	5.68	4.54	1.10	.	.	+ .2	.	.
<i>Linum perenne</i>
<i>Lygodesmia juncea</i>	.	2.10
<i>Medicago sativa</i>
<i>Melilotus albus</i>	3.18	23.52	1.4	1.4
<i>Melilotus officinalis</i>	25.86	55.92	26.90	9.46	+ .4
<i>Monarda fistulosa</i>	4.14	1.6	1.4	.	1.14	.	.	.
Mosses & Lichens	1.2	.	3.4
<i>Osmorhiza longistylis</i>
<i>Oxalis stricta</i>	1.10	1.16	1.8	+ .2
<i>Parietaria pennsylvanica</i>	1.16	4.42	+ .2
Polypodiaceae	+ .8	1.14	4.6	.	.
<i>Ranunculus abortivus</i>	2.18	+ .10
<i>Ratibida columnifera</i>
<i>Sanicula marilandica</i>	2.4	1.18	.	.	.	19.70
<i>Smilacina stellata</i>	+ .8	3.18	+ .8	1.10	.	.	1.10	2.30	7.46	6.56	2.30	+ .6
<i>Smilax herbacea</i>	+ .6	+ .2	.	+ .2	.	.
<i>Solidago missouriensis</i>	.	.	.	+ .4
<i>Solidago rigida</i>	+ .4	.	.	.
<i>Taraxacum officinale</i>	+ .2	.	+ .6	+ .4	1.26	1.26	2.22	+ .6	+ .4	1.10	.	.
<i>Thalictrum dasycarpum</i>	2.18	3.22	+ .2	.
<i>Thalictrum venulosum</i>	.	.	.	+ .2	.	.	1.4	+ .2	.	.	2.10	.
<i>Thermopsis rhombifolia</i>	.	.	+ .2	1.8	.	.	.
<i>Tragopogon dubius</i>	+ .2	2.10	+ .2	.	.	+ .2	.
<i>Trifolium pratense</i>	2.16	4.16
<i>Urtica dioica</i>	.	.	1.4	1.6	1.4	+ .6	1.8	1.14	.	1.10	4.24	.
<i>Vicia americana</i>	1.8	.	+ .4
<i>Viola pratensis</i>	+ .12	+ .4	+ .2	+ .4
<i>Viola</i> sp.	+ .2	.	+ .2	.	.	.
Species in microplots	25	26	26	20	24	19	28	25	31	27	20	16
Coverage of shrubs	53	23	119	112	37	87	23	38	106	60	123	77
Coverage of graminoids	105	116	25	11	44	58	126	101	37	35	11	0
Coverage of forbs	35	89	34	16	45	29	24	18	20	59	55	39
Total coverage	193	228	178	139	126	164	173	157	163	154	189	116

Table A8.—*Juniperus scopulorum*/*Oryzopsis micrantha* habitat type

	Stand number						
	33	34	37	38	49	50	53
Location							
Quarter section	SW	SW	NW	SE	SW	SW	NE
Section	11	11	24	23	30	30	25
Township	140N	140N	140N	140N	148N	148N	148N
Range	101W	101W	101W	101W	99W	99W	100W
Topographic position							
Slope (%)	45	65	42	38	47	67	64
Aspect (°)	332	2	296	11	304	294	358
Elevation (m)	817	792	786	826	634	655	652
Coverage/Frequency							
SHRUBS							
<i>Artemisia cana</i>
<i>Artemisia frigida</i>	.	.	+ .4
<i>Artemisia tridentata</i>	+ .2	+ .2	+ .2
<i>Ceratoides lanata</i>
<i>Chrysothamnus nauseosus</i>	.	.	+ .2
<i>Clematis ligusticifolia</i>
<i>Gutierrezia sarothrae</i>
<i>Potentilla fruticosa</i>	+ .2
<i>Prunus virginiana</i>	48.50	.	14.44	4.22	6.22	+ .2	2.8
<i>Rhus aromatica</i>	11.36	+ .2	12.36	2.10	2.8	3.6	+ .6
<i>Ribes odoratum</i>	+ .2	2.4
<i>Ribes setosum</i>	.	1.2
<i>Rosa arkansana</i>	+ .4
<i>Rosa woodsii</i>	+ .6	.	1.6	1.4	.	.	.
<i>Symphoricarpos occidentalis</i>	+ .8	3.10	3.34	2.20	4.24	1.8	+ .12
GRAMINOIDS							
<i>Agropyron caninum</i>	+ .4	+ .2	+ .2	5.26	+ .2	+ .2	.
<i>Carex eburnea</i>	6.10	4.8
<i>Oryzopsis micrantha</i>	59.99	62.99	68.99	68.98	59.96	77.99	76.99
<i>Poa pratensis</i>	+ .2
<i>Stipa viridula</i>
FORBS							
<i>Achillea millefolium</i>	+ .12	+ .8	2.22	+ .8	+ .2	+ .6	+ .8
<i>Anemone patens</i>	+ .6
<i>Antennaria rosea</i>	.	+ .2	+ .2	.	+ .4	+ .6	+ .12
<i>Astragalus adsurgens</i>	.	.	.	+ .6	.	.	.
<i>Campanula rotundifolia</i>	+ .2	+ .4	1.16	1.18	+ .12	3.32	3.28
<i>Chenopodium album</i>	.	.	.	+ .2	.	.	.
<i>Fragaria virginiana</i>	+ .2	.	+ .2
<i>Galium boreale</i>	5.60	4.34	3.72	5.68	5.66	3.40	7.72
<i>Gentianella amarella</i>	.	+ .2	+ .4	.	.	.	1.14
<i>Geum triflorum</i>	+ .2	.
<i>Hackelia deflexa</i>	+ .6
<i>Heuchera richardsonii</i>	+ .4	.	.	.	+ .2	.	.
<i>Linum perenne</i>
<i>Melilotus officinalis</i>
<i>Mirabilis linearis</i>	.	.	.	+ .6	.	.	.
<i>Monarda fistulosa</i>	1.4
Mosses & Lichens	78.99	92.99	91.99	37.80	78.99	69.99	61.98
<i>Opuntia fragilis</i>
<i>Opuntia polyacantha</i>
<i>Oxytropis campestris</i>	.	.	+ .2
<i>Oxytropis lambertii</i>	.	1.4	+ .2
<i>Parietaria pennsylvanica</i>
Polypodiaceae	.	2.40	1.22	1.20	1.18	1.8	7.76
<i>Potentilla pensylvanica</i>
<i>Selaginella densa</i>
<i>Smilacina stellata</i>	2.18	+ .2	1.12	+ .4	1.10	.	1.10
<i>Solidago missouriensis</i>	+ .2	.	.	+ .6	.	.	1.6
<i>Taraxacum officinale</i>	.	.	+ .10	+ .10	+ .10	+ .6	+ .6
<i>Tragopogon dubius</i>	.	.	.	+ .2	.	.	.
<i>Vicia americana</i>	+ .2	.
<i>Viola adunca</i>	.	.	+ .6	1.20	+ .6	1.28	+ .14
<i>Viola</i> sp.
Species in microplots	20	15	19	19	15	17	20
Coverage of shrubs	59	6	30	9	12	4	2
Coverage of graminoids	59	62	68	73	59	83	80
Coverage of forbs	86	99	99	45	85	77	81
Total coverage	204	167	197	127	156	164	163

Table A9.—*Symphoricarpos occidentalis* community type

	Stand number				
	11	17	19	45	59
Location					
Quarter section	NW	NE	SE	SE	NW
Section	23	33	28	29	28
Township	140N	141N	141N	147N	148N
Range	102W	101W	101W	100W	100W
Topographic position					
Slope (%)	11	8	3	4	6
Aspect (°)	335	347	165	18	160
Elevation (m)	707	716	704	719	719
Coverage/Frequency					
SHRUBS					
<i>Artemisia cana</i>	.	+ .2	.	.	.
<i>Artemisia frigida</i>	.	+ .4	.	.	.
<i>Prunus americana</i>	.	.	1.2	.	.
<i>Prunus virginiana</i>	.	.	3.4	.	.
<i>Ribes odoratum</i>	6.8
<i>Rosa woodsii</i>	37.60	2.8	2.10	+ .2	.
<i>Symphoricarpos occidentalis</i>	89.99	85.99	95.99	98.99	98.99
GRAMINOIDS					
<i>Agropyron caninum</i>	.	1.6	11.22	1.4	.
<i>Agropyron smithii</i>	15.28	63.82	10.20	1.2	.
<i>Andropogon gerardii</i>	1.6
<i>Bromus inermis</i>	.	.	6.6	.	.
<i>Bromus tectorum</i>	.	.	.	+ .6	.
<i>Carex filifolia</i>	.	+ .2	.	.	.
<i>Elymus virginicus</i>	.	.	1.6	.	.
<i>Koeleria pyramidata</i>	.	+ .2	.	.	.
<i>Poa pratensis</i>	.	.	64.86	6.22	21.46
<i>Stipa viridula</i>	.	1.8	.	.	.
FORBS					
<i>Achillea millefolium</i>	+ .2	2.12	+ .6	.	+ .2
<i>Artemisia ludoviciana</i>	9.24	2.12	1.14	1.16	3.14
<i>Astragalus agrestis</i>	.	8.42	.	.	.
<i>Chenopodium album</i>	.	.	+ .2	+ .2	.
<i>Convolvulus arvensis</i>	1.4	.	+ .2	4.20	.
<i>Convolvulus sepium</i>	1.8
<i>Galium aparine</i>	+ .2	.	+ .2	+ .6	.
<i>Galium boreale</i>	.	.	6.16	8.24	10.42
<i>Hackelia deflexa</i>	+ .2
<i>Humulus lupulus</i>	.	.	9.14	.	.
<i>Lactuca oblongifolia</i>	11.44	1.22	38.90	+ .2	.
<i>Linum perenne</i>	.	2.18	.	.	.
<i>Linum rigidum</i>	+ .2
<i>Medicago sativa</i>	.	.	.	+ .2	.
<i>Parietaria pennsylvanica</i>	5.16	7.24	1.8	4.8	+ .4
<i>Ratibida columnifera</i>	+ .2
<i>Sisymbrium altissimum</i>	.	.	.	+ .2	.
<i>Taraxacum officinale</i>	+ .6	.	+ .2	+ .4	.
<i>Thalictrum venulosum</i>	+ .2
<i>Urtica dioica</i>	.	.	+ .2	.	.
Species in microplots	14	15	20	16	10
Coverage of shrubs	132	87	101	98	98
Coverage of graminoids	15	65	92	8	22
Coverage of forbs	26	22	55	17	14
Total coverage	173	174	248	123	134

APPENDIX 2. TREE POPULATION ANALYSES

Population structure of trees in stands, by habitat types. Numbers of trees listed per 375 m², with basal area for the stand as m²/ha given below the stand number. Abbreviations of tree species are as follows:

ACNE—*Acer negundo*
CRCH—*Crataegus chrysocarpa*
FRPE—*Fraxinus pennsylvanica*
JUSC—*Juniperus scopulorum*
PODE—*Populus deltoides*
POTR—*Populus tremuloides*
ULAM—*Ulmus americana*

Table A10.—Population structure of trees in stands, by habitat type

Stand and b.a.	Spp.	Diameter (at breast height) classes in dm							
		0-1		1-2	2-3	3-4	4-5	5-6	6-7
		<.5	>.5						
1. <i>Fraxinus pennsylvanica</i> / <i>Symphoricarpos occidentalis</i> habitat type									
29	FRPE	56							
39.5	JUSC	20	6	15					
	PODE						4	5	
30	FRPE	5							
23.3	JUSC	20	4	2	1				
	PODE						3	3	
51	FRPE	513	31	2					
63.1	JUSC	33	1	5					
	PODE							3	4
52	FRPE	489	8						
39.5	JUSC	6	9	4	1				
	PODE				4	3	3	1	
2. <i>Fraxinus pennsylvanica</i> / <i>Prunus virginiana</i> habitat type									
41	FRPE	332	20	28	5				
23.8	JUSC	6		1					
42	FRPE	306	11	12	8	1			
21.6	JUSC			1					
57	FRPE	15	5	17	9	4			
35.9	ULAM	66			2	1			
	JUSC	2							
58	FRPE	5	1	15	3				
25.1	ULAM	21	8	15	4				
	ACNE	8	1	1					
	JUSC	2							
3. <i>Populus tremuloides</i> / <i>Betula occidentalis</i> habitat type									
43	POTR	81	58	9					
14.7	FRPE	47	10	2					
	JUSC	7							
60	POTR	82	35	28	1				
21.1	FRPE	41							
	ULAM	9	1	2					
	CRCH	1							
67	POTR	136	15	32					
20.9	FRPE	61	6	2					
	JUSC	1							
68	POTR	22	2	17	22				
41.8	FRPE	92	5	6					
	ACNE	13	5						
4. <i>Juniperus scopulorum</i> / <i>Oryzopsis micrantha</i> habitat type									
33	JUSC	47	21	20	1	3			
29.6	FRPE	62	15	5					
34	JUSC	126	60	30	1				
23.4									
37	JUSC	112	82	24					
22.1	FRPE	17	1						
38	JUSC	98	86	30					
25.4	FRPE	6							
49	JUSC	207	108	10	2				
22.2	FRPE	1							
50	JUSC	158	43	26	4				
22.7	FRPE	2							
53	JUSC	232	59	21	3				
22.4	FRPE	10							

APPENDIX 3. SOIL ANALYSES

Table A11.—Results of soil analyses of the upper 1 dm of mineral soil from each stand. Data are arranged according to habitat types

Stand	pH	C.E.C. (meq/ 100 g)	Free lime ¹	Extractable cations (meq/100 g)			P (ppm)	N (%)	O.M. ² (%)	Mechanical analysis (percent)			
				Ca	Mg	Na				Sand	Silt	Clay	Texture
Stipa comata/Carex filifolia habitat type													
27	6.2	-	-	-	-	-	-	0.174	2.6	56.4	34.0	9.6	Sandy loam
35	6.9	-	-	-	-	-	-	0.116	1.8	64.4	29.6	6.0	Sandy loam
36	6.7	6.84	-	7.65	3.58	0.14	4.5	0.097	2.0	71.4	22.6	6.0	Sandy loam
39	7.5	6.47	+	16.67	3.54	0.18	3.0	0.107	1.4	74.0	18.0	8.0	Sandy loam
40	7.1	-	-	-	-	-	-	0.073	1.0	79.0	13.0	8.0	Loamy sand
56	7.1	-	-	-	-	-	-	0.114	1.6	53.6	35.6	10.8	Sandy loam
61	6.8	9.61	+	51.10	1.73	0.07	4.0	0.081	1.3	86.0	7.6	6.4	Loamy sand
Agropyron smithii/Carex filifolia habitat type													
3	7.7	-	-	-	-	-	-	0.159	2.4	32.4	45.0	22.6	Loam
5	7.7	-	-	-	-	-	-	0.180	2.6	39.4	40.0	20.6	Loam
14	7.6	18.38	+++	39.05	2.47	0.12	0.5	0.178	2.7	38.8	37.6	23.6	Loam
18	7.7	13.83	+++	26.66	3.98	0.10	0.5	0.178	2.4	45.2	35.2	19.6	Loam
20	7.7	-	-	-	-	-	-	0.171	2.2	50.4	32.0	17.6	Loam
21	7.7	-	-	-	-	-	-	0.149	2.0	43.4	40.6	16.0	Loam
48	7.6	-	-	-	-	-	-	0.153	1.8	50.0	36.0	14.0	Loam
54	6.7	28.47	-	11.54	4.79	0.11	1.0	0.181	2.1	44.0	41.0	15.0	Loam
62	7.6	-	-	-	-	-	-	0.137	2.0	35.0	40.6	24.4	Loam
Andropogon scoparius/Carex filifolia habitat type													
8	7.7	-	-	-	-	-	-	0.164	2.6	66.4	26.0	7.6	Sandy loam
15	7.7	9.07	+++	26.05	1.35	0.11	0.5	0.158	2.1	61.2	31.2	7.6	Sandy loam
22	7.7	-	-	-	-	-	-	0.237	3.0	34.4	49.6	16.0	Loam
23	7.7	14.11	++	30.01	3.12	0.15	3.0	0.190	2.4	48.4	41.6	10.0	Loam
24	7.7	-	-	-	-	-	-	0.155	2.2	52.4	40.0	7.6	Sandy loam
46	7.7	-	-	-	-	-	-	0.154	2.1	22.6	55.0	22.4	Silt loam
55	7.8	-	-	-	-	-	-	0.087	1.1	23.6	49.6	26.8	Loam
63	7.6	-	-	-	-	-	-	0.142	2.0	57.0	28.6	14.4	Loam
64	7.6	11.32	+++	24.45	3.51	0.07	0.5	0.123	1.8	48.4	38.6	13.0	Loam
Juniperus horizontalis/Andropogon scoparius habitat type													
9	7.6	-	-	-	-	-	-	0.112	2.4	40.4	37.4	22.2	Loam
10	7.6	17.88	+++	54.16	3.30	0.25	0.5	0.232	3.4	26.4	44.0	29.6	Clay loam
12	7.4	26.67	++	34.03	2.74	0.04	1.0	0.219	3.0	48.8	29.6	21.6	Loam
44	7.3	39.13	+	36.89	6.37	0.27	2.0	0.274	4.2	48.0	41.0	11.0	Loam
47	7.5	-	-	-	-	-	-	0.138	2.5	37.6	34.0	28.4	Clay loam
Artemisia tridentata/Agropyron smithii habitat type													
4	7.4	26.42	+	43.17	6.97	1.57	6.0	0.147	3.6	23.0	35.4	41.6	Clay
13	7.1	-	-	-	-	-	-	0.146	3.5	24.8	71.6	3.6	Silt loam
16	7.5	10.31	+	20.45	5.81	0.71	2.0	0.165	2.2	39.2	35.2	25.6	Loam
28	7.6	31.02	+++	32.04	4.61	1.30	1.0	0.177	2.5	26.0	41.6	32.4	Clay loam
Artemisia cana/Agropyron smithii habitat type													
1	7.8	15.98	+++	39.22	2.69	2.61	2.5	0.100	1.8	18.4	50.0	31.6	Silty clay loam
6	7.8	-	-	-	-	-	-	0.157	2.0	14.4	50.0	35.6	Silty clay loam
7	7.8	-	-	-	-	-	-	0.137	1.9	13.4	52.0	34.6	Silty clay loam
26	7.7	-	-	-	-	-	-	0.098	2.9	40.4	46.6	13.0	Loam
66	8.0	-	-	-	-	-	-	0.069	1.7	17.8	63.6	18.6	Silt loam
69	7.8	11.31	+++	23.61	3.21	1.11	24.0	0.071	1.4	13.8	61.6	24.6	Silt loam
70	7.7	-	-	-	-	-	-	0.046	1.7	58.8	29.6	11.6	Sandy loam
2	7.6	11.22	+++	33.52	2.42	0.11	1.0	0.101	2.1	38.4	29.0	32.6	Clay loam
25	7.6	-	-	-	-	-	-	0.098	2.2	34.4	47.6	18.0	Loam
31	7.7	8.82	+++	20.18	3.39	0.25	0.5	0.082	2.0	38.0	42.0	20.0	Loam
32	7.7	-	-	-	-	-	-	0.055	1.6	36.0	54.0	10.0	Silt loam
65	7.6	-	-	-	-	-	-	0.088	3.6	34.8	50.6	14.6	Silt loam
Fraxinus pennsylvanica/Symphoricarpos occidentalis habitat type													
29	7.6	17.57	++	21.13	3.13	0.31	2.5	0.138	2.6	31.0	51.0	18.0	Silt loam
30	7.6	-	-	-	-	-	-	0.089	1.7	44.0	41.0	15.0	Loam
51	7.5	28.21	++	30.31	6.42	0.59	1.0	0.152	2.6	31.0	35.0	34.0	Clay loam
52	7.5	17.14	+	27.91	6.61	0.23	2.0	0.155	3.4	22.0	50.6	27.4	Clay loam

Table A11.—Results of soil analyses of the upper 1 dm of mineral soil from each stand.

Data are arranged according to habitat types—Continued

Stand	pH	C.E.C. (meq/ 100 g)	Free lime ¹	Extractable cations (meq/100 g)			P (ppm)	N (%)	O.M. ² (%)	Mechanical analysis (percent)			Texture
				CA	Mg	Na				Sand	Silt	Clay	
Fraxinus pennsylvanica/Prunus virginiana habitat type													
41	7.6	-	-	-	-	-	-	0.202	2.9	33.0	33.0	34.0	Clay loam
42	7.6	15.25	+ + +	32.23	4.97	0.25	0.5	0.154	2.5	15.0	39.0	46.0	Clay
57	6.0	25.53	-	18.52	6.83	0.12	9.5	0.362	4.1	34.6	45.6	19.8	Loam
58	6.4	24.83	-	17.72	3.89	0.10	9.5	0.406	3.6	38.0	43.2	18.8	Loam
Populus tremuloides/Betula occidentalis habitat type													
43	7.2	12.94	-	13.56	4.89	0.13	3.0	0.099	2.3	35.0	39.0	26.0	Loam
60	5.7	-	-	-	-	-	-	0.221	3.3	48.0	34.6	17.4	Loam
67	6.0	18.23	-	13.98	6.05	0.08	9.0	0.111	1.9	64.4	24.0	11.6	Sandy loam
68	7.1	16.66	-	12.53	4.06	0.11	1.0	0.103	1.6	32.8	39.6	27.6	Clay loam
Juniperus scopulorum/Oryzopsis micrantha habitat type													
33	6.7	-	-	-	-	-	-	0.295	4.3	57.0	33.0	10.0	Sandy loam
34	7.9	17.58	+ + +	27.62	8.10	1.57	0.5	0.130	2.3	25.0	39.0	36.0	Clay loam
37	7.8	-	-	-	-	-	-	0.167	3.0	27.0	34.0	39.0	Clay loam
38	7.6	30.91	-	19.43	13.91	3.55	0.5	0.203	3.3	31.0	30.0	39.0	Clay loam
49	7.6	-	-	-	-	-	-	0.180	3.0	26.0	39.0	35.0	Clay loam
50	7.8	-	-	-	-	-	-	0.149	3.3	35.0	36.0	29.0	Clay loam
53	7.8	23.09	+	25.80	8.22	1.32	0.5	0.164	2.6	44.0	32.0	24.0	Loam
Symphoricarpos occidentalis community type													
11	7.4	-	-	-	-	-	-	0.259	3.1	45.8	28.6	25.6	Loam
17	7.5	15.93	+ + +	28.11	2.90	0.17	2.5	0.222	3.0	47.2	31.2	21.6	Loam
19	7.5	-	-	-	-	-	-	0.341	4.2	18.0	48.0	34.0	Silty clay loam
45	6.2	23.90	-	16.43	5.92	0.10	2.5	0.286	3.4	32.4	45.6	22.0	Loam
59	5.8	-	-	-	-	-	-	0.273	3.3	35.0	46.2	18.8	Loam

¹Free lime determined subjectively. + = low, + + = medium, + + + = high.²Organic matter.

Table A12.—Gravel content (percent by weight) of soil samples taken from the upper 1 dm of mineral soil from each stand

Habitat type	Stand	Gravel content
<i>Stipa comata</i> / <i>Carex filifolia</i>	61	11.4
<i>Andropogon scoparius</i> / <i>Carex filifolia</i>	22	6.7
<i>Andropogon scoparius</i> / <i>Carex filifolia</i>	23	36.2
<i>Andropogon scoparius</i> / <i>Carex filifolia</i>	24	30.3
<i>Juniperus horizontalis</i> / <i>Andropogon scoparius</i>	10	6.5
<i>Juniperus horizontalis</i> / <i>Andropogon scoparius</i>	44	29.2
<i>Artemisia tridentata</i> / <i>Agropyron smithii</i>	28	4.6
<i>Artemisia cana</i> / <i>Agropyron smithii</i>	2	16.0



Hansen, Paul L., George R. Hoffman, and Ardell J. Bjugstad. 1984. The vegetation of Theodore Roosevelt National Park, North Dakota: A habitat type classification. General Technical Report RM-113, 35 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Vegetation of the Theodore Roosevelt National Park, North Dakota, was characterized according to habitat type based on concepts and methods developed by Daubenmire. Ten habitat types—three grassland and seven wooded types—were described including a key to identify the habitat types.

Keywords: Vegetation classification, habitat type, *Stipa comata*, *Carex filifolia*, *Andropogon scoparius*, *Juniperus horizontalis*, *Artemisia tridentata*, *Agropyron smithii*, *Artemisia cana*, *Fraxinus pennsylvanica*, *Symphoricarpos occidentalis*, *Prunus virginiana*, *Populus tremuloides*, *Betula occidentalis*, *Juniperus scopulorum*, *Oryzopsis micrantha*

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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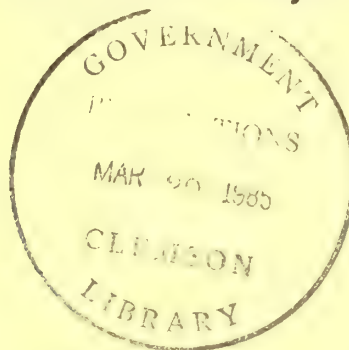
Fort Collins,
Colorado 80526

General Technical
Report RM-114



Silvical Characteristics of Engelmann Spruce

Robert R. Alexander and Wayne D. Shepperd



Abstract

This report summarizes information on distribution, botanical description, habitat conditions, life history, special uses, and genetics of Engelmann spruce.

Silvical Characteristics of Engelmann Spruce

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Contents

	Page
DISTRIBUTION	1
BOTANICAL DESCRIPTION	1
HABITAT CONDITIONS	2
Climate	2
Soils	3
Topography	3
Associated Vegetation	4
Trees	4
Understory Vegetation	4
LIFE HISTORY	5
Reproduction and early growth	5
Flowering and Fruiting	5
Seed Production	5
Seed Dissemination	6
Seedling Development	6
Vegetative Reproduction	9
Sapling and Pole Stage to Maturity	9
Growth and Yield	9
Rooting Habit	10
Reaction to Competition	10
Silvicultural Systems and Cutting Methods	12
Damaging Agents	12
PROPERTIES AND USES OF THE WOOD	14
GENETICS	14
Population Differences	14
Races and Hybrids	14
LITERATURE CITED	15
APPENDIX: Habitat types, community types and plant communities in which <i>Picea engelmannii</i> is a major climax, co-climax, minor climax, or ma- jor seral	20

Silvical Characteristics of Engelmann Spruce

Robert R. Alexander and Wayne D. Shepperd

Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) is one of seven species of spruce indigenous to the United States (Little 1979). Other common names are Columbian spruce, mountain spruce, white spruce, silver spruce, and pino real (fig. 1).

Engelmann spruce—subalpine fir (*Abies lasiocarpa* Hook.) Nutt.) forests occupy the highest water yielding areas in the Rocky Mountains. They also provide timber, habitats for a wide variety of game and nongame wildlife, forage for livestock, and recreational opportunities and scenic beauty (Alexander 1977). However, these values are indigenous to where spruce grows rather than to any special properties associated with Engelmann spruce.

DISTRIBUTION

Engelmann spruce is widely distributed in the western United States and two provinces in Canada



Figure 1.—Mature Engelmann spruce on the Fraser Experimental Forest, Colorado.

(Little 1971). Its range extends from British Columbia and Alberta, Canada, south through all western states to New Mexico and Arizona (fig. 2).

In the Pacific Northwest, Engelmann spruce grows along the east slope of the Coast Range from west-central British Columbia, south along the crest and east slope of the Cascades through Washington and Oregon to northern California (Alexander 1958, 1965, 1980). It is a minor component of these high elevation forests.

Engelmann spruce grows in the Rocky Mountains of southwestern Alberta, south through the high mountains of eastern Washington and Oregon, Idaho, western Montana, to western and central Wyoming, and in the high mountains of southern Wyoming, Colorado, Utah, eastern Nevada, New Mexico, and northern Arizona (Alexander 1958, 1965, 1980). It is a major component of the high elevation Rocky Mountain forests.

BOTANICAL DESCRIPTION

The botanical features of Engelmann spruce, as described by McSwain et al. (1970) and Preston (1948), are as follows:

Needles.—Needles are 1 to 1-1/4 inches long, petioled, flexible, four-sided, usually blue green with an occasional whitish glaucous bloom. Tips are blunt or acute. Needles tend to be crowded on the upper side of the branch because those on the lower side are curved upwards (fig. 3A).

Flowers.—Male flowers are dark purple; female, bright scarlet. Each is borne separately in the crown (fig. 3A).

Cones.—The cones are usually 1 to 2-1/2 inches long, light chestnut brown when ripe, and ovate to cylindrical in shape. Cones are sessile or short-stalked with thin, somewhat papery, wedge-shaped scales, commonly notched at the apex (fig. 3B).

Seeds.—The dark brown to nearly black seeds average 1/8 inch long, with a broad oblique wing about 1/2 inch long (fig. 3B).

Twigs.—The minutely pubescent, rather stout twigs are orange brown to gray brown.

Winter buds.—The pale chestnut brown winter buds are broadly ovoid to conic, and average 1/8 to 1/4 inch long.

Bark.—The bark is very thin and broken into large, purplish-brown to russet-red, loosely attached scales (fig. 3C).

Wood.—Heartwood is nearly white with an occasional tinge of red. Sapwood is narrow—3/4 to 2 inches wide in sawtimber—and difficult to distinguish from heartwood, but it is commonly lighter in color. The wood is generally straight-grained, lightweight, medium stiff, soft, fine-textured, and without odor or taste. It has

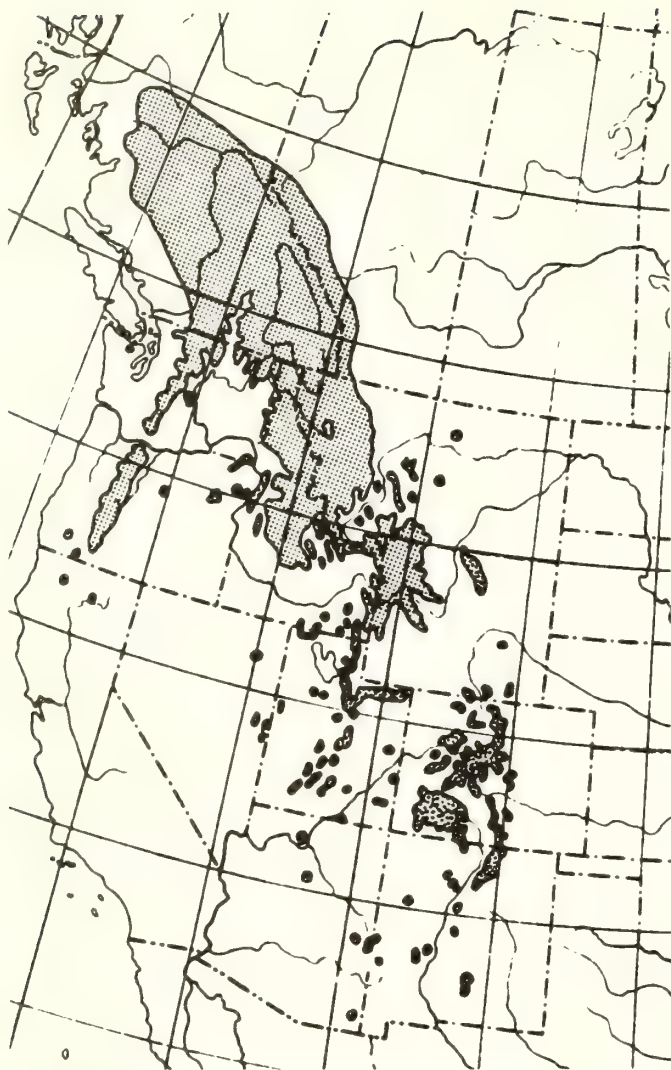


Figure 2.—Natural range of Engelmann spruce. (Little 1971)

moderately low shrinkage, can be readily air-dried, and is easy to work. Resin ducts are few, but distinguish the wood from true firs.

HABITAT CONDITIONS

Climate

Engelmann spruce grows in a cool and humid climate, with long, cold winters and short, cool summers (Thornthwaite 1948). It occupies one of the highest and coldest forest environments in the western United States, characterized by heavy snowfall and temperature extremes of more than -50°F to above 90°F . Climatic data for four subregions of the United States within the species range are given in table 1 (Baker 1944, Haefner 1971, Marr et al. 1968).

The range of mean annual temperatures is narrow considering the wide distribution of the species. Average annual temperatures are near freezing and frost may occur any month of the year. Average precipitation exceeds 24 inches annually, with only

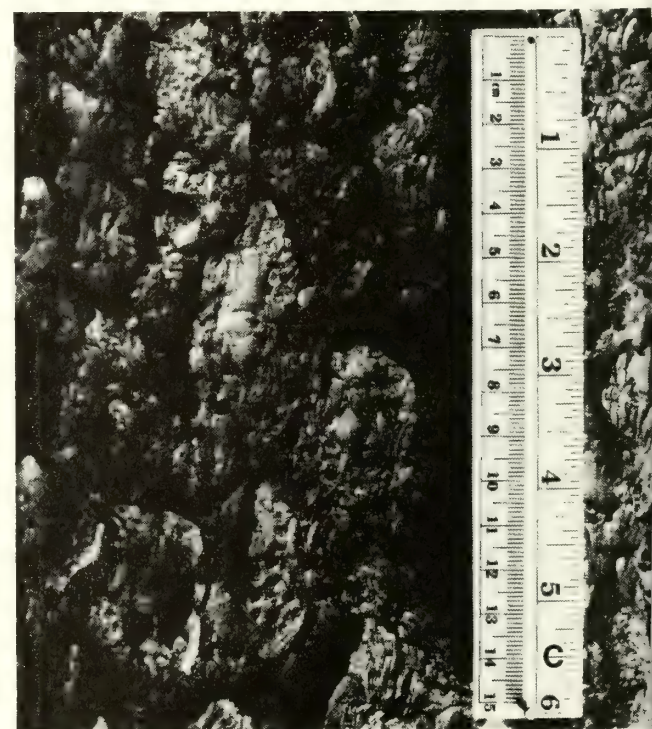
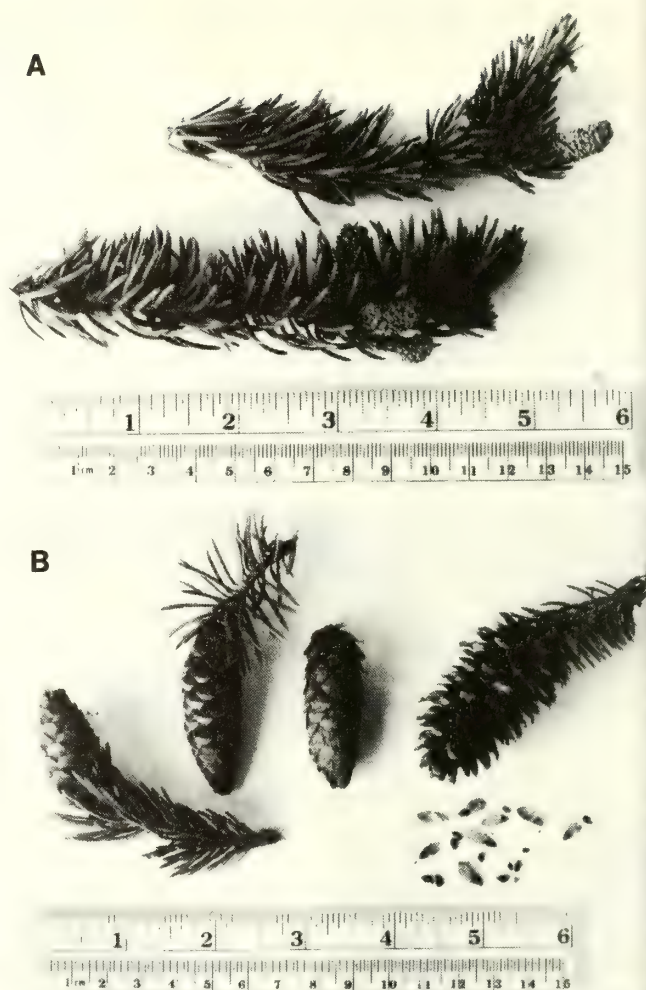


Figure 3.—Botanical features of Engelmann spruce: A, needles and male flowers; B, mature and immature cones and seeds; C, bark.

Table 1.—Climatological data for four regional subdivisions within the range of Engelmann spruce

Location	Average temperature			Annual precipitation	Annual snowfall	Frostfree period
	Annual	July	January			
	°F	°F	°F	inches	inches	days
Pacific Northwest	35	50-55	15-20	60-160	400 +	45-90
U.S. Rocky Mountains						
Northern ¹	30-35	45-55	10-20	24-45 +	250 +	⁴ 30-60
Central ²	30-35	50-55	10-15	24-55	150-350 +	⁴ 30-60
Southern ³	35	50-60	15-20	24-35 +	200 +	⁴ 30-60

¹Includes the Rocky Mountains of Montana and Idaho and associated mountains of eastern Washington and Oregon.

²Includes the Rocky Mountains of Wyoming and Colorado and associated mountains of Utah.

³Includes the Rocky Mountains and associated ranges of New Mexico and Arizona and the plateaus of southern Utah.

⁴Frost may occur any month of the year.

moderate or no seasonal deficiency. Summer is the driest season in the Cascades and Rocky Mountains west of the Continental Divide south to southwestern Colorado. The mountains east of the divide, in southwestern Colorado, southern Utah, and in New Mexico and Arizona, receive considerable summer rainfall, while winter snowfall can be relatively light (Baker 1944, Johnson and Cline 1965, Marr 1961, Thornthwaite 1948). Winds are predominately from the west and southwest and can be highly destructive to Engelmann spruce (Alexander 1964, Alexander and Buell 1955, Aubenmire 1943).

Soils

Information on soils where Engelmann spruce grows is limited. In the Pacific Coast region, soil parent materials are mixed and varied. Country bedrock is composed of a variety of sedimentary, igneous, and metamorphic rock. The most common of the great soil groups are Cryorthods (Podzolic soils), Haplumbrepts (Western Brown forest soils), Haplorthods (Brown Podzolic soils), Hapludalfs (Gray-Brown Podzolic soils), and Aploxerults and Haplohumults (Reddish-Brown Lateric soils); these great soil groups developed from deep alluvial and lacustrine deposits, deep residual material weathered in place from country rock, and volcanic lava and ash. Xerochrepts (Regosolic soils) developed from shallow residual material are also widespread. Xeromments (Regosolic soils) and Haplaquolls (Humic Gley soils) are the principal soils derived from alluvium. On the east side of the Cascade crest, soils are largely Aploxeralfs (Non-Calcic Brown soils) and Haploxerolls (chestnut soils) (Franklin and Dyrness 1973, USDA SCS 1975).

In the Rocky Mountain subalpine zone, soil materials vary according to the character of the bedrock from which they originated. Crystalline granite rock predominates, but conglomerates, shales, sandstones, salts, and andesites commonly occur. Glacial deposits and stream alluvial fans are also common along valley

bottoms. Of the great soils group, Cryorthods (Podzolic soils) and Haplorthods (Brown Podzolic soils) occur extensively on all aspects. Dystrochrepts (Sols Brun Acides) occur extensively on the drier aspects. Aquods (Ground-Water Podzolic soils) are found in the more poorly drained areas, Eutroboralfs (Gray-Wooded soils) are found where timber stands are less dense and parent material finer textured. Eutrochrepts (Brown Forest soils) occur mostly in the lower subalpine along stream terraces and side slopes. Lithics (Lithosolic soils) occur whenever bedrock is near the surface. Dystrandrepts (Bog soils), and Haplaquepts (Humic Gley soils) occur extensively in poorly drained upper stream valleys (Johnson and Cline 1965, USDA SCS 1975).

Regardless of the great soil groups associated with spruce stands, it grows best on moderately deep, well-drained, loamy sands and silts, and silt and clay loam soils developed from volcanic lava flows and sedimentary rock. Good growth is also made on alluvial soils developed from a wide range of parent materials, where an accessible water table is more important than physical properties of the soil. It does not grow well on shallow, dry, coarse-textured sands; gravels developed primarily from granitic and schistic rock; coarse sandstones and conglomerates; rocky glacial till; heavy clay surface soils; or saturated soils (Alexander 1958, 1965).

Topography

Along the east slope of the Coast Range and interior valleys of southwestern British Columbia, Engelmann spruce grows at 2,500 to 3,500 feet. Farther south in the Cascade Mountains of Washington and Oregon, it generally grows at 4,000 to 6,000 feet, but may be found at 8,000 feet on sheltered slopes, and at 2,000 feet in cold pockets along streams and valley bottoms. In northern California, it is found at 4,000 to 5,000 feet (Alexander 1980, Sudworth 1916).

South of the Peace River Plateau in the Canadian Rocky Mountains of western British Columbia and Alberta, Engelmann spruce grows at 2,500 to 6,000 feet;

in the Rocky Mountains of Idaho and Montana, and in the adjacent mountains of eastern Washington and Oregon, at 2,000 to 9,000 feet. But above 6,000 to 7,500 feet, it is a minor component of the stand, and below 5,000 feet it is confined to moist, lower slopes and cold, valley bottoms (Alexander 1958, 1965).

Engelmann spruce is found at 9,000 to 11,000 feet in the Rocky Mountains of Utah, Wyoming, and Colorado, but may extend as low as 8,000 feet along cold stream bottoms and to timberline at 11,500 feet. In the Rocky Mountains of New Mexico and Arizona and on the plateaus of southern Utah, it grows at 9,500 to 11,000 feet but may grow as low as 8,000 feet and as high as 12,000 feet (Bates 1924, Marr 1961, Pearson 1931).

Associated Vegetation

Trees

Engelmann spruce most typically grows together with subalpine fir to form the Engelmann spruce—subalpine fir type (SAF Type 206) (Society of American Foresters 1980). It may also occur in pure or nearly pure stands. Spruce grows in 15 other forest cover types recognized by the Society of American Foresters, usually as a minor component or in frost pockets:

SAF Type Number	Type
201 ———	White Spruce
205 ———	Mountain Hemlock
208 ———	Whitebark Pine
209 ———	Bristlecone Pine
210 ———	Interior Douglas-fir
212 ———	Western Larch
213 ———	Grand Fir
215 ———	Western White Pine
216 ———	Blue Spruce
217 ———	Aspen
218 ———	Lodgepole Pine
219 ———	Limber Pine
224 ———	Western Hemlock
226 ———	Coastal True Fir—Hemlock
227 ———	Western Redcedar—Western Hemlock

Composition of forests in which Engelmann spruce grows is influenced by elevation, aspect, and latitude (Daubenmire 1943).² In the Rocky Mountains and Cascades, subalpine fir is its common associate at all elevations. In the northernmost part of its range along the Coast Range and in the Rocky Mountains of Canada, it mixes with white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill. B.S.P.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.). In the Rocky Mountains of Montana and Idaho, in the Cascades, and in the mountains of

eastern Washington and Oregon, associates at lower and middle elevations are western white pine (*Pinus monticola* Dougl. ex D. Don), western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Biessn.) Franco), western larch (*Larix occidentalis* Nutt.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud). Associates at higher elevations are Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr), subalpine larch (*Larix lyallii* Parl.), and whitebark pine (*Pinus albicaulis* Engelm.).

In the Rocky Mountains south of Montana and Idaho and in the mountains of Utah, lodgepole pine, Rocky Mountain Douglas-fir, blue spruce (*Picea pungens* Engelm.), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), quaking aspen (*Populus tremuloides* Michx.), and occasionally ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and southwestern white pine (*Pinus strobiformis* Engelm.) are common associates at lower and middle elevations, and corkbark fir (*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.), limber pine (*Pinus flexilis* James), and bristlecone pine (*Pinus aristata* Engelm.) at higher elevations. Engelmann spruce extends to timberline in the Rocky Mountains south of Idaho and Montana and may form pure stand at timberline in the southernmost part of its range. In the Canadian Rockies of southwestern Alberta and adjacent British Columbia and into the Rocky Mountains north of Wyoming and Utah, and the Cascades, spruce usually occupies moist sites below timberline; its high elevation associates form timberline forests (Alexander 1958, 1965, 1980).

Understory Vegetation

In the understory throughout much of the range of Engelmann spruce, Rocky Mountain maple (*Acer glabrum* Torr.), twinflower (*Linnaea borealis* L.), and heartleaf arnica (*Arnica cordifolia* Hook.) occur on cool, moist sites; myrtle boxleaf (*Pachistima myrsinites* (Pursh.) Raf.), elksedge (*Carex geyeri* Boott), and creeping juniper (*Juniperus communis* L.) occur on warm, dry sites; and grouse whortleberry (*Vaccinium scoparium* Michx.), mountain gooseberry (*Ribes montigenum* McClat.), and fireweed (*Epilobium angustifolium* L.) occur on cool, dry sites.

Species characteristically found in the Pacific Northwest Region, and the Rocky Mountains and associated ranges north of Utah and Wyoming include: Labrador tea (*Ledum glandulosum* Nutt.), Cascades azalea (*Rhododendron albiflorum* Hook.), rusty skunkbush (*Meziasia ferruginea* Smith), and woodrush (*Luzula hitcockii* Hamet-Ahti) on cool, moist sites; starry solomonic plume (*Smilacina stellata* (L.) Desf.), queenscup beadli (*Clintonia uniflora* (Schult.) Runth), twistedstalk (*Streptopus amplexifolius* (L.) D.C.), and sweetscented bedstraw (*Galium triflorum* Michx.) on warm, moist sites; dwarf huckleberry (*Vaccinium caespitosum* Michx.), and blue huckleberry (*Vaccinium globula*

²Classification of forest vegetation into "habitat types" based on methodology developed by Daubenmire (1952) and modified by others is available for much of the western forested lands. The known habitat types for all lands where Engelmann spruce grows are listed in the appendix, with other descriptive material.

Rydb.) on cool, dry sites; beargrass (*Xerophyllum tenax* Pursh.) Nutt.), white spirea (*Spiraea betulifolia* Hook.), pinegrass (*Calamagrostis rubescens* Buckl.), and big whortleberry (*Vaccinium membranaceum* Dougl.) on warm, dry sites; and marshmarigold (*Caltha leptosepala* J.C.), devilsclub (*Oplopanax horridum* (J.E. Smith) Miq.), and bluejoint reedgrass (*Calamagrostis canadensis* Michx.) Beauv.) on wet sites (Daubenmire and Daubenmire 1968, Franklin and Dyrness 1973, Pfister 1972, Pfister et al. 1977, Steele et al. 1981, 1983).

Understory vegetation characteristically found in the Rocky Mountains and associated ranges south of Idaho and Montana include: mountain bluebells (*Mertensia siliata* (James) G. Don) and heartleaf bittercress (*Cardamine cordifolia* Gray) on cool, moist sites; red buffaloberry (*Shepherdia canadensis* (L.) Nutt.), Oregon grape (*Berberis repens* Lindl.), daisy fleabane (*Erigeron superus* Rydb.), and Arizona peavine (*Lathyrus arizonicus* Britt.) on warm, dry sites; and Rocky Mountain whortleberry (*Vaccinium myrtillus* L.), groundsel (*Senecio anguisorboides* Rydb.), polemonium (*Polemonium pulcherrimum* Hook.), prickly currant (*Ribes lacustre* Pers.) Poir), sidebells pyrola (*Pyrola secunda*), and mosses on cool, dry sites (Alexander et al. 1984a, Hess 1981, Hoffman and Alexander 1976, 1980, 1983, Moir and Ludwig 1979, Wirsing and Alexander 1975).

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting

Engelmann spruce is monoecious, with ovulate strobili usually borne in the upper crown and staminate strobili in branchlets in the lower crown (Fowler and Roche 1977). Separation of male and female strobili within a crown is an important mechanism for preventing self-fertilization. Male flowers ripen and pollen is wind-disseminated in late May and early June at lower elevations and from mid-June to early July at higher elevations. Cones mature in August and early September the same year, and seeds ripen from late August to late September. Cones are shed during the fall and winter of the first year (Alexander 1958, 1965, Schmidt and Lotan 1980, USDA Forest Service 1974).

Seed Production

Although open-grown Engelmann spruce begin bearing cones when they are 4 to 5 feet tall and 15 to 40 years old, seed production does not become significant until trees are larger and older. The most abundant crops in natural stands are produced on healthy, vigorous, dominant trees 15 inches or more in diameter at breast height and 150 to 250 years old. Engelmann spruce is rated as a moderate to good seed producer (Alexander 1958, 1965, Alexander, et al. 1982, Hodson and Foster 1910, USDA Forest Service 1974). Good to bumper seed crops, based on the following criteria, are

generally borne every 2 to 5 years, with some seed produced almost every year (Alexander and Noble 1976):

Number of sound seeds per acre	Seed crop rating
0-10,000	Failure
10,000-50,000	Poor
50,000-100,000	Fair
100,000-250,000	Good
250,000-500,000	Heavy
> 500,000	Bumper

There is considerable variation in seed production from year to year and from area to area. In one study in Colorado covering 42 area-seed-crop years, 12 were rated good to bumper and 30 fair to failure (Noble and Ronco 1978). In another Colorado study covering 10 years and 13 locations, seed production was rated good or better in 6 years, and fair to failure in 4 years (Alexander et al. 1982). In an earlier study in Montana, 22 cone crops observed during a 45-year period west of the Continental Divide were rated as 5 good, 8 fair, and 9 poor. East of the Divide seed production was poorer; only 2 good and 4 fair years were reported for a 21-year period, while 15 were failures (Boe 1954). In other studies in Montana and the Intermountain Region, seed production was rated good to bumper in 1 year out of 5 with the other 4 years rated as failures (Roe 1967, Squillace 1954). Variability in seed quality accentuates differences in seed production. The proportion of sound seed is usually highest in years of highest seed production (Alexander et al. 1982).

Observations in spruce forests before seedfall have indicated that part of each seed crop is lost to cone and seed insects (Alexander 1974). In a recently completed study in Colorado, insect-caused loss in Engelmann spruce averaged 28% of the total seed produced during a 4-year period (1974-1977) (Schmid et al. 1981). The percentage of infested cones was highest during years of poor seed production. The primary seed-eating insects were a spruce seedworm (*Cydia youngana* Kearfott = (*Laspeyresia youngana*)) and an unidentified species of fly, possibly a *Hylemya*, found only in the larval stage.

Some loss of seed results from cutting and storing of cones by pine squirrels (*Tamiasciurus hudsonicus fremonti* Audubon and Bachman), but the actual quantitative loss is unknown. After seed is shed, small mammals such as deer mice (*Peromyscus maniculatus* Wagner), red-backed mice (*Clethrionomys gapperi* Vigors), mountain voles (*Microtus montanus* Peale), and chipmunks (*Eutamias minimus* Bachman) are the principal source of seed loss. Undoubtedly mammals consume considerable seed, but the magnitude of losses is not known and results of studies on protecting seed are conflicting. For example, in western Montana spruce seedling success was little better on protected than unprotected seed spots (Schopmeyer and Helmers 1947), but in British Columbia, protection of spruce seed from rodents was essential to spruce regeneration success (Smith 1955).

Seed Dissemination

Most seed is shed by the end of October, although some falls throughout the winter. The small, winged seeds are light, averaging about 135,000 per pound (USDA Forest Service 1974). Practically all of the seed is disseminated by wind. Squirrels, other mammals, and birds are not important in seed dispersal.

Seed is dispersed long distances only in years of bumper seed crops. For example, studies in the Rocky Mountains show that 96,000 to 250,000 sound seeds per acre were dispersed 400 to 600 feet from the windward source into clearcut blocks 600 to 800 feet wide (Noble and Ronco 1978, Roe 1967). Seedfall in uncut stands ranged from 500,000 to 5,000,000 seeds per acre. In years of good to heavy seed crops—100,000 to 500,000 sound seeds per acre—seedfall into cleared openings diminished rapidly as distance from seed source increased. Prevailing winds influence the pattern of seedfall into openings 200 to 800 feet across. The amount of seed dispersed to the windward timber edge is about 80% of the seedfall under the uncut stand. About 40% of the amount of seedfall under uncut windward stands is dispersed as far as 100 feet (Alexander 1969, Alexander and Edminster 1983, Noble and Ronco 1978). Seedfall then diminishes steadily but at a less rapid rate of decline as distance increases to about two-thirds of the way—150 to 600 feet—across the openings. At those distances, the average number of seeds falling varies from about 25% (at 150 feet) to less than 5% (at 600 feet) of the number released in the uncut stand. Beyond this point, seedfall gradually increases toward the leeward timber edge, but is only about 30% of the seedfall along the windward edge (Alexander 1969, Alexander and Edminster 1983).

Seedling Development

Germination and Establishment.—Viability of Engelmann spruce seed is rated good and the vitality persistent. The average germinative capacity of spruce is higher than that of many associated species, as shown in the following tabulation (USDA Forest Service 1974).

Species	Average germinative capacity percent
Engelmann spruce	69
Subalpine fir	31–34
Lodgepole pine	65–80
Western white pine	44
Rocky Mtn. Douglas-fir	60–93
Western larch	57
Grand fir	46–57
Western hemlock	53–56
Pacific silver fir	20–26
White fir	30–37

Viable seeds of spruce that survive over winter normally germinate following snowmelt, when seedbeds are moist and air temperatures are at least 45° F. Field germination of spruce over long periods of time in Colorado has ranged from 0 to 28% of the sound seeds dispersed, depending upon the seedbed and environmental factors (Alexander 1984, Noble and Alexander 1977).

In the undisturbed forest, spruce seeds germinate and seedlings become established on duff, litter, partially decomposed humus, decaying wood, and mounds of mineral soil upturned by windthrown trees. Any disturbance that removes the overstory produces new microhabitats (Roe et al. 1970). Under these latter circumstances, germination and initial establishment is generally better on mineral soil and mixed mineral soil and humus seedbeds because moisture conditions are more stable (Alexander 1984, Boyd and Deitschman 1969, Day 1964, Noble and Alexander 1977, Roe and Schmidt 1964). Decayed wood, the natural forest floor, and undisturbed duff and litter are poor seedbeds because they dry out rapidly (Alexander 1984, Day 1964, Noble and Alexander 1977, Roe et al. 1970, Smith 1955). Spruce seedling establishment on burned seedbeds has been variable. Success is related to severity of burn, depth of ash, and amount of exposed mineral soil (Clark 1969, Roe et al. 1970, Shearer 1984). Once established (at least 3 years old), seedling ability to survive is not increased by a mineral soil seedbed, but is favored by adequate soil moisture, cool temperatures, and shade.

Engelmann spruce will germinate in all light intensities found in nature, but 40% to 60% of full shade is most favorable for seedling establishment at high elevations. Light intensity and solar radiation are high at elevations and latitudes where spruce grows in the central and southern Rocky Mountains, and seedlings do not establish readily in the open. Planted seedlings often develop a chlorotic appearance that has been attributed to solarization—a phenomenon by which light intensity inhibits photosynthesis and which ultimately results in death (Ronco 1970). Mortality can be reduced by shading seedlings. At lower elevations and higher latitudes in the northern Rocky Mountains, spruce can become established and survive in the open. Spruce can establish and survive better in lower light intensities than its common, intolerant associates such as lodgepole pine, Rocky Mountain Douglas-fir, and aspen, but at extremely low light intensities it cannot compete favorably with such shade-enduring associates as the true firs and hemlocks (Alexander 1958, 1965, Bates 1925).

Engelmann spruce is restricted to cold, humid habitats because of its low tolerance to high temperature and drought (Bates 1923, Helmers et al. 1970). Solar radiation at high elevations heats soil surfaces up to 150° F and higher and increases water losses from both seedlings and soil by transpiration and evaporation (Alexander 1984, Noble and Alexander 1977, Roe et al. 1970).

Because of its slow initial root penetration and extreme sensitivity to heat in the succulent stage, drought and heat-girdling cause substantial first-year spruce

seedling mortality (Alexander 1984, Day 1963, Noble and Alexander 1977).

Tree seedlings in the succulent stage are particularly susceptible to stem-girdling. The cortex is killed by a temperature of 130° F, but prolonged exposures to lower temperatures may also be lethal. On the Fraser Experimental Forest, heat-girdling was an important cause of early seedling mortality on unshaded seedbeds (Alexander 1984, Noble and Alexander 1977). Soil surface temperatures exceeded 150° F in the open on a north aspect and 160° on a south aspect at 10,500 feet elevation in the month of June. Maximum air temperature during this period did not exceed 78° F. In western Montana, at lower elevations, soil surface temperatures exceeded 160° F on gentle north slopes several times during one summer (Roe et al. 1970). Early shade protection improved survival of newly germinated spruce seedlings; 30% to 50% of the seedlings were lost to heat-girdling on unshaded plots, compared to 10% on shaded plots. Day (1963) studied heat and drought mortality of newly germinated spruce seedlings in southwestern Alberta, and found that when water was excluded nearly three-fourths of the mortality on four different unshaded seedbed types was caused by heat-girdling. Surface temperatures as low as 113° F caused heat girdling, but losses were not high until soil surface temperatures were above 122° F. Shading reduced heat-girdling on all seedbed types. Soil surface temperatures in excess of lethal levels for spruce seedlings, especially on burned seedbeds, have been reported in British Columbia (Smith 1955).

Air and soil temperatures (below the surface) are not usually directly responsible for seedling mortality, but they affect growth. Helmers et al. (1970) studied the growth of Engelmann spruce seedlings under 30 different combinations of day and night temperatures. They found that the greatest height and root growth, and top and root dry matter production was with a diurnal variation of 66° F (air and soil) day temperatures and 73° F (air and soil) night temperatures. Shepperd (1981), using the same night temperature regime, raised the day soil temperature to 73° F and significantly increased root growth.

Frost can occur any month of the growing season where spruce grows. It is most likely to occur in depressions and cleared openings because of cold air drainage and radiation cooling. Newly germinated spruce seedlings are most susceptible to early fall frosts. In a greenhouse and laboratory study, new seedlings did not survive temperatures as low as 15° F until about 10 weeks old (Noble 1973a). Terminal bud formation began at 8 weeks; buds were set and needles were mature at 10 to 12 weeks after germination.

After the first year, seedlings are most susceptible to frost early in the growing season when tissues are succulent. Shoots are killed or injured by mechanical damage resulting when tissue freezes and thaws. Frost damage has been recorded in most years in Colorado (Ronco 1967). In light frost years damage was minor, but heavy frosts either damaged or killed all new shoots of open-grown seedlings.

In the early fall, the combination of warm daytime temperatures, nighttime temperatures below freezing, and saturated soil unprotected by snow are conducive to frost-heaving. On the Fraser Experimental Forest, Colorado, these conditions generally occurred in about 1 out of 2 years (Alexander 1984, Noble and Alexander 1977). Frost-heaving has been one of the principal causes of first-year seedling mortality on scarified seedbeds on the north aspect (Alexander 1984). Furthermore, seedlings continue to frost-heave after four growing seasons. Shading has reduced losses by reducing radiation cooling.

The moisture condition of the seedbed during the growing season largely determines first-year seedling survival. On some sites in the central Rocky Mountains, summer drought is responsible for substantial first-year mortality, especially in years when precipitation is low or irregular. On the Fraser Experimental Forest in the central Rocky Mountains, drought and desiccation have caused more than half of the first-year seedling mortality on a south aspect, and nearly two-thirds of the total after 5 years (Alexander 1984). On a north aspect during the same period, drought has accounted for about 40% of first-year seedling mortality, and more than one-half of the mortality at the end of 5 years.

In the northern Rocky Mountains, late spring and early summer drought is a serious threat most years to first-year seedlings. In western Montana, all seedlings on one area were killed by drought in a 2-week period in late summer when their rate of root penetration could not keep pace with soil drying during a prolonged dry period (Roe et al. 1970). Late spring and early summer drought is also a serious cause of first-year seedling mortality in the southern Rockies. Drought losses can continue to be significant throughout the Rocky Mountains during the first 5 years of seedling development, especially during prolonged summer dry periods (Alexander 1984, Noble and Alexander 1977).

The moisture provided by precipitation during the growing season is particularly critical to seedling survival during the first year. Alexander and Noble (1971) studied the effects of amount and distribution of moisture on seedling survival in the greenhouse. Treatments simulated common summer precipitation patterns in north-central Colorado. They concluded that, under favorable seedbed and environmental conditions: (1) at least 1 inch of well-distributed precipitation is needed monthly before seedlings will survive drought; (2) with this precipitation pattern, more than 1.5 inches of monthly rainfall is not likely to increase seedling survival; but (3) few seedlings will survive drought with less than 2 inches of rainfall monthly when precipitation comes in only one or two storms.

Summer precipitation may not always benefit seedling survival and establishment. Summer storms in the Rocky Mountains may be so intense that much of the moisture runs off, especially from bare soil surfaces. Moreover, soil movement on unprotected seedbeds buries some seedlings and uncovers others (Roe et al. 1970).

Understory vegetation can be either a benefit or serious constraint to spruce seedling establishment (Alexander 1966, Day 1964, Ronco 1972). Spruce seedlings become established more readily on sites protected by willows (*Salix* spp.), shrubby cinquefoil (*Potentilla fruticosa* L.), fireweed, and dwarf whortleberry than in the open. Because these plants compete less aggressively for available soil moisture than those listed below, the net effect of their shade is beneficial to seedling survival. In contrast, mortality occurs when spruce seedlings start near clumps of grass or sedges or scattered herbaceous plants such as mountain bluebells, currants (*Ribes* spp.), and Oregon grape that compete severely for moisture and smother seedlings with cured vegetation when compacted by snow cover.

The only significant biotic factor affecting spruce regenerating success on a long-term study on the Fraser Experimental Forest was birds. About 15% to 20% of the total mortality resulted from the clipping of cotyledons on newly germinated seedlings by grey-headed juncos (*Junco caniceps* Woodhouse) (Alexander 1984, Noble and Alexander 1977, Noble and Shepperd 1973).

Damping-off, needlecast, snowmold, insects, rodents, and trampling and browsing by large animals also kill spruce seedlings, but losses are no greater than for any other species (Alexander 1958, 1965).

The number of seeds required to produce a first-year seedling and an established seedling (at least 3 years old) and the number of first-year seedlings that produce

an established seedling vary considerably, depending upon seed production, distance from source, seedbed, and other environmental conditions. In one study in clearcut openings in Colorado during the period 1961-1975, covering a wide variety of conditions, on the average 665 sound seeds (range 60-2,066) were required to produce a single first-year seedling, and 6,800 (range 926-20,809) to produce a seedling 4 or more years old. An average of 21 first-year seedlings was necessary to produce a single seedling 4 or more years old, although as few as 4 and as many as 24 first-year seedlings survived under different conditions (Noble and Ronco 1978).

Aspect and cultural treatments can also be important factors in the successful establishment of Engelmann spruce. In another Colorado study, an average of 18 sound seeds was required to produce a single first-year seedling on shaded, mineral soil seedbeds on a north aspect; and 32 sound seeds to produce a 5-year-old seedling. In contrast, 156 seeds were required to produce a first-year seedling on shaded, mineral soil seedbeds on a south aspect, and 341 seeds to produce a 5-year-old seedling (Alexander 1983, 1984). Shearer (1984) studying the effects of prescribed burning and wildfire after clearcutting on regeneration in the western larch type in Montana also found that natural and planted spruce survived better on the north aspect than on the south aspect.

Environmental conditions favorable and unfavorable to the establishment of Engelmann spruce natural regeneration are summarized in figure 4.

REGENERATION CONDITIONS			
FAVORABLE		UNFAVORABLE	
a	>250,000 seed/acre	SEED CROP	<50,000 seed/acre
b	North and East	ASPECT	South and West
c	Ambient air >32°F night and <78°F day; maximum surface <90°F	TEMPERATURES	Ambient air <32°F night and >78°F day; maximum surface >90°F
d	>0.50 in. week	PRECIPITATION	<0.40 in. week
e	Light-textured, sandy-loam	SOIL	Heavy-textured, clay-loam
f	>40% exposed mineral soil	SEEDBED	<20% exposed mineral soil
g	50-70% dead shade		<30% dead shade
h	<2 in. duff and litter		>4 in. duff and litter
i	Light vegetative cover <30% non sod-forming		Heavy vegetative cover >60% sod-forming
j	Seedlings >12 weeks old by mid-Sept	SURVIVAL	Seedlings <12 weeks old by mid-Sept
k	Low population of birds and small mammals that eat tree seed and young seedlings		High population of birds and small mammals that eat tree seed and young seedlings
l	Protection from trampling		No protection from trampling
m	Fall snow cover when frost heaving conditions exist		No fall snow cover when frost heaving conditions exist
n	No late lying spring snowfields when conditions favorable to snowmold exist		Late lying spring snowfields when conditions favorable to snowmold exist

Figure 4.—Environmental conditions favorable and unfavorable to Engelmann spruce regeneration.

If trees are well distributed, stocking should not exceed about 600 to 800 stems per acre at age 30 years (Alexander and Edminster 1980, Edminster 1978). In order to obtain proper distribution and full utilization of the site however, at least 1,000 stems per acre should be established initially. This will allow for subsequent mortality and permit later thinning to obtain proper spacing and to select future crop trees.

Early Growth.—The early growth of Engelmann spruce is very slow (LeBarron and Jemison 1953). First-year spruce seedlings grown on mineral soil seedbeds under partial shade in Colorado have a rooting depth of 3 to 4 inches, with a total root length of 5 inches (Noble 1973b). In the Rocky Mountains of Arizona and New Mexico, root depths of vigorous one-year-old seedlings have been reported to average about 2.8 inches on shaded, mineral soil seedbeds, and on seedbeds where the depth of humus was about 1 inch (Jones 1971). Observations in the Rocky Mountains of Idaho and Montana, and in British Columbia indicate that first-year penetration of spruce seedlings averages only about 1.5 inches (Roe et al. 1970, Smith 1955).

Initial shoot growth of natural seedlings is equally slow in Colorado. First-year spruce seedlings are seldom over 1 inch tall. After 5 years, seedlings average 1 to 3 inches in height under natural conditions and 2 to 4 inches in height on both partially shaded and unshaded, prepared, mineral soil seedbeds. Seedlings 10 years old may be only 6 to 8 inches tall under natural conditions and 10 to 12 inches tall on both partially shaded and unshaded, mineral soil seedbeds³ (fig. 5). After 10 years, trees grow at a more rapid rate, averaging about 4 to 5 feet in height in about 20 years in full sun or light overstory shade and, reaching about the same height after 40 years under moderate overstory shade. Severe

suppression of seedling growth occurs at low light levels. It is not uncommon to find trees 100 years old and only 3 to 5 feet tall under the heavy shade of a closed forest canopy.

Seedling growth has been somewhat better elsewhere in the Rocky Mountains, especially at lower elevations and higher latitudes. For example, in one study in the Intermountain west, average annual shoot growth of natural 10-year-old seedlings averaged 4.5 inches on clearcut areas, and 3.2 inches on areas with a partial overstory (McCoughey and Schmidt 1982). Planted spruces, 5 to 8 years old, averaged 20 to 24 inches in height in Utah.⁴ In Montana, planted spruces have been reported to reach breast height (4.5 feet) in about 10 years.⁵

Early diameter growth of Engelmann spruce is less affected by competition for growing space than that of its more intolerant associates. In a study of seed spot density in northern Idaho, diameter growth of spruce seedlings after 17 years was only slightly greater on thinned seed spots, and height growth was unaffected by the thinning. In contrast, diameter and height growth of western white pine increased significantly as the number of seedlings per seed spot decreased (Roe and Boe 1952).

Vegetative Reproduction

Engelmann spruce can reproduce by layering (Hodson and Foster 1910). It most often layers near timberline where the species assumes a dwarfed or prostrate form. Layering can also occur when only a few trees survive fires or other catastrophies. Once these survivors have increased to the point where their numbers alter the microenvironment to improve germination and establishment, layering diminishes. In general, this form of reproduction is insignificant in establishing and maintaining closed forest stands (Oosting and Reed 1952).

Sapling and Pole Stage to Maturity

Growth and Yield

Natural Stands.—Engelmann spruce is one of the largest of the high mountain species. Under favorable conditions, average stand diameter will vary from 15 to 30 inches and average dominant height from 45 to 130 feet, depending upon site quality and density³ (fig. 6). Individual trees may exceed 40 inches in diameter and 160 feet in height (LeBarron and Jemison 1953). Engelmann spruce is a long-lived tree, maturing in about 300 years. Dominant spruces are often 250 to 450 years old, and trees 500 to 600 years old are not uncommon.

⁴Personal correspondence with Dr. Wyman C. Schmidt, Principal Silviculturist, FS-INT-RWU 1251, Intermountain Forest and Range Experiment Station, Bozeman, Mont.

⁵Personal correspondence with Mr. Orville Engelby, Assistant Director, Timber Management (silviculture), USDA Forest Service, R-4 Intermountain Region, Ogden, Utah.



Figure 5.—Engelmann spruce seedlings on mineral soil seedbeds average only 8 to 12 inches in height after 10 years.

Engelmann spruce has the capacity to make good growth at advanced ages. If given sufficient growing space, it will continue to grow steadily in diameter for 300 years, long after the growth of most associated trees species slows down (Alexander 1958, 1965, LeBarron and Jemison 1953).

Yields are usually expressed for the total stand. Engelmann spruce does not normally grow in pure stands but in varying mixtures with associated species. Average volumes per acre in old-growth (normally 250 to 350 years old) spruce-fir forests in the Rocky Mountains, may be practically nothing at timberline, 5,000 to 15,000 board feet on poor sites, and 25,000 to 40,000 board feet on better sites. Volumes as high as 80,000 to 100,000 board feet per acre have been reported for very old stands on exceptional sites (Pearson 1931, Thompson 1929). Average annual growth in virgin spruce-fir forests will vary from a net loss due to mortality to 80 to 200 board feet per acre, depending upon age, density, and vigor of the stand (Miller and Choate 1964). Engelmann spruce usually constitutes at least 70% and often more than 90% of the basal area in trees 5 inches d.b.h. and larger in these stands (Oosting and Reed 1952).



Figure 6.—Dominant Engelmann spruce on the Fraser Experimental Forest, Colorado. Tree is 18 inches in diameter, over 90 feet tall, and 250 years old at d.b.h.

Managed Stands.—With prompt restocking after timber harvest and periodic thinning to control stand density, growth of individual spruce trees and yields of spruce-fir stands can be greatly increased compared with unmanaged stands, and the time required to produce these volumes and sizes can be reduced. For example, in stands managed at the growing stock levels considered optimum for timber production (GSL 140 to 180) on 140- to 160-year rotations with a 20-year thinning interval, average volumes per acre will range from 30,000 to 40,000 board feet on poor sites to 90,000 to 105,000 board feet per acre on good sites (Alexander and Edminster 1980). Volume production substantially declines on all sites when growing stock level is reduced below the optimum for timber production, and the decline is greater with each successive reduction in GSL (table 2). Average annual growth will vary from 180 to 650 board feet per acre depending upon growing stock level, site quality, cutting cycle, and rotation age (Alexander and Edminster 1980). Moreover, since most subalpine fir will be removed in early thinnings, these yields will be largely from Engelmann spruce.

Rooting Habit

Engelmann spruce is considered to have a shallow root system. The weak tap root of seedlings does not persist beyond the juvenile stage, and when trees grow where the water table is near the surface or on soils underlain by impervious rock or clay hardpans, the weak, superficial lateral root system common to the seedling stage may persist to old age. Under these conditions, most roots are in the first 12 to 18 inches of soil. But where spruce grows on deep, porous, well-drained soils, the lateral root system may penetrate to a depth of 8 feet or more (Alexander 1958, 1965).

Reaction to Competition

Engelmann spruce is rated tolerant in its ability to endure shade (Baker 1949). It is definitely more shade enduring than Rocky Mountain Douglas-fir, western white pine, lodgepole pine, aspen, western larch, or ponderosa pine but less so than subalpine fir (the most common associate throughout much of its range), grand fir, white fir, and mountain hemlock. Engelmann spruce is either a co-climax with subalpine fir or long-lived seral forest vegetation throughout much of its range. In the Rocky Mountains of British Columbia and Alberta and south of Montana and Idaho, Engelmann spruce and subalpine fir occur as either codominants or in nearly pure stands of one or the other. In the Rocky Mountains of Montana and Idaho, and in Utah, eastern Oregon, and Washington, subalpine fir is the major climax species. Engelmann spruce may also occur as a major climax species, but more often it is a persistent long-lived seral species. Pure stands of either species can be found however (Alexander 1980).

Although spruce-fir forests form climax or near-climax vegetation associations, they differ from most climax forests in that all stands are not truly all-age

Table 2.—Estimated board-foot volume production per acre of spruce-fir in relation to growing stock level, site index, rotation age, and cutting cycle with a clearcut option (trees 8 inches d.b.h. and larger to a 6-inch top) (Alexander and Edminster 1980)

Rotation age	Cutting cycle	Growing stock level							
		40	60	80	100	120	140	160	180
----- years -----		----- thousand board feet -----							
Site index 50									
100	20	7.1	8.9	10.4	11.6	12.0	11.7	11.4	10.9
120		9.2	12.1	14.6	16.4	17.4	17.8	17.4	16.2
140		11.2	14.8	18.1	21.0	22.8	23.7	23.9	23.1
160		13.3	17.9	21.8	25.3	27.8	29.4	30.9	29.9
100	30	7.5	9.1	10.5	11.4	11.6	11.4	11.0	10.3
120		10.0	12.7	15.1	16.8	17.5	17.4	17.2	16.1
140		12.2	15.7	18.8	21.1	23.1	23.5	23.5	22.5
160		14.6	19.0	22.7	26.4	28.6	29.8	30.2	28.8
Site index 60									
100	20	9.1	12.0	14.1	16.1	17.0	17.4	17.6	17.0
120		11.6	15.6	19.2	21.8	23.6	25.2	26.2	25.8
140		14.1	19.3	23.8	27.2	29.7	31.6	33.3	34.3
160		16.6	22.9	28.3	32.6	36.0	39.2	41.3	42.4
100	30	9.8	12.5	14.3	15.6	16.5	17.0	17.0	16.3
120		12.8	17.0	20.4	22.6	24.0	25.4	26.2	25.2
140		15.4	20.6	25.1	28.6	31.5	33.7	34.9	33.7
160		18.1	24.2	29.1	33.9	37.9	40.8	42.4	41.4
Site index 70									
100	20	11.7	15.0	17.9	20.6	23.0	24.7	25.4	24.9
120		14.8	19.2	23.6	27.6	31.2	34.1	36.1	35.8
140		17.6	23.8	29.1	34.3	38.9	42.7	45.1	46.2
160		20.6	27.7	34.2	40.6	46.6	50.7	54.2	56.8
100	30	12.4	16.2	19.2	21.6	23.2	24.3	24.6	24.1
120		16.1	21.7	26.0	29.6	32.8	34.8	35.5	34.8
140		19.0	25.5	31.6	36.9	40.7	43.4	44.7	45.1
160		22.1	29.8	37.1	43.0	48.2	52.3	54.9	56.5
Site index 80									
100	20	13.8	18.2	22.2	26.0	29.6	32.5	34.3	34.1
120		17.4	23.9	29.4	34.2	38.6	43.7	46.4	47.4
140		20.7	28.8	35.7	41.6	47.5	52.9	57.0	60.1
160		24.3	33.4	41.8	49.0	56.0	62.6	68.2	72.6
100	30	15.5	20.0	24.2	27.8	30.6	30.4	33.5	33.0
120		19.8	25.7	31.8	37.4	41.8	45.0	46.4	45.7
140		23.2	31.4	38.1	44.8	50.1	54.6	57.8	58.5
160		27.0	33.3	45.6	53.6	60.2	65.9	69.8	71.2
Site index 90									
100	20	16.4	22.6	27.8	32.1	35.9	39.1	42.5	44.5
120		20.4	28.6	35.4	41.3	46.9	52.0	56.2	59.9
140		24.2	33.9	42.3	50.1	57.4	63.7	69.3	74.2
160		28.2	39.4	49.4	58.7	67.2	74.7	82.2	89.0
100	30	18.7	25.2	20.7	35.5	39.3	42.2	43.8	43.2
120		23.5	31.9	39.7	46.6	52.2	56.4	58.9	58.2
140		27.4	37.2	46.9	55.6	62.6	68.3	72.1	73.1
160		31.7	43.2	54.4	65.0	73.6	80.6	85.8	87.0
Site index 100									
100	20	19.6	26.6	32.7	38.4	43.6	48.2	51.8	54.2
120		24.2	33.2	41.5	49.0	56.0	62.4	68.0	71.6
140		28.6	39.5	49.8	59.2	68.0	76.0	83.2	88.1
160		33.1	45.8	57.8	68.5	79.4	88.8	97.6	104.6
100	30	21.9	29.2	36.3	43.3	48.7	52.6	54.2	53.6
120		27.6	37.9	47.6	56.3	63.2	69.2	72.1	71.4
140		32.1	44.4	56.0	66.4	75.3	82.7	87.4	88.9
160		36.6	51.2	64.5	76.5	87.7	96.6	103.0	104.8

(LeBarron and Jemison 1953). Some stands are clearly single-storied, indicating that desirable spruce forests can be grown under even-aged management. Other stands are two- or three-storied, and multistoried stands are not uncommon (Alexander 1974). These may be the result of either past disturbances such as fire, insect epidemics, or cutting, or the gradual deterioration of old-growth stands associated with normal mortality from wind, insects, and diseases. The latter circumstance is especially evident in the formation of some multistoried stands. On the other hand, some multistoried stands appear to have originated as uneven-aged stands and are successfully perpetuating this age-class structure (Hanley et al. 1975).

Climax forests are not easily displaced by other vegetation, but fire, logging, and insects have played an important part in the successional status and composition of spruce-fir forests. Complete removal of the stand by fire or logging results in such drastic environmental changes that spruce and fir are usually replaced by lodgepole pine, aspen, or shrub and grass communities (Roe et al. 1970, Stahelin 1943). The kind of vegetation initially occupying the site usually determines the length of time it takes to return to a spruce-fir forest. It may vary from a few years if the site is initially occupied by lodgepole pine or aspen to as many as 300 years if grass is the replacement community (fig. 7).

The ecophysiology of Engelmann spruce in relation to its common associates is becoming better understood. Kaufmann (1975, 1976, 1979, 1982a, 1982b, 1984a, 1984b), Kaufmann and Troendle (1981), and Kaufmann et al. (1982) summarized what is known about the utilization of water by Engelmann spruce as follows: (1) leaf water potential decreases in proportion to the transpiration rate but is influenced by soil temperature and water supply; (2) needle water vapor conductance (directly proportional to stomatal opening) is controlled primarily by visible irradiance and absolute humidity difference from needle to air (evaporative demand), with secondary effects from temperature and water stress; (3) nighttime minimum temperatures below 39° F retard stomatal opening the next day, but stomata function well from early spring to late fall, and high transpiration rates occur even with considerable snowpack on the ground; (4) leaf water vapor conductance is higher in

Engelmann spruce than in subalpine fir, but lower than in lodgepole pine or aspen; (5) Engelmann spruce trees have less total needle area per unit area of sapwood water conducting tissue than subalpine fir but more than lodgepole pine or aspen; and (6) Engelmann spruce trees have a greater needle area per unit of bole or stand basal area than subalpine fir, lodgepole pine, or aspen. At equal basal area, annual canopy transpiration of spruce is about 80% greater than lodgepole pine, 50% greater than subalpine fir, and 220% greater than aspen. These high rates of transpiration cause Engelmann spruce to occur primarily on the wetter sites.

Silvicultural Systems and Cutting Methods

Both even- and uneven-aged silvicultural systems are appropriate for use in Engelmann spruce forests, but not all cutting methods under each system are applicable in every stand nor will every cutting method meet specific management objectives (Alexander 1977, Alexander and Engelby 1983). The even-aged cutting methods include clearcutting, which removes all trees in strips, patches, blocks, or stands with a single cut (fig. 8); and shelterwood cutting, which removes trees in one, two or three cuts (fig. 9) and its modifications. Because of susceptibility to windthrow, the seed-tree method is not a suitable way to regenerate spruce. The seedbed is prepared for regeneration after clearcutting, or after the seed cut with shelterwood cutting, by various methods ranging from burning and mechanical scarification, to only that associated with logging activity (Alexander 1974, Alexander and Engelby 1983).

The uneven-aged cutting methods appropriate to spruce are individual tree and group selection cuttings (fig. 10) and their modifications, which remove selected trees in all size classes at periodic intervals over the entire area or in groups up to 2 acres in size. Reproduction occurs continuously, but methods of site preparation are limited.

Shelterwood and individual tree selection cutting methods will favor associated species such as true firs and hemlocks over spruce. Clearcutting and group selection cutting methods will favor Engelmann spruce over these more tolerant associates but will increase the proportion of intolerant associates like lodgepole pine and Douglas-fir.

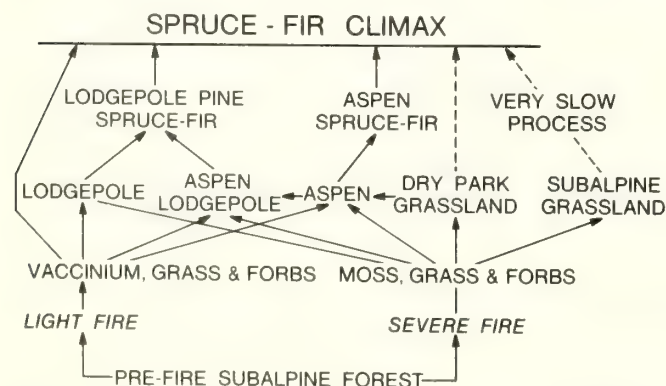


Figure 7.—Natural succession in Rocky Mountain subalpine spruce-fir forests after fire.

Damaging Agents

Windfall.—Engelmann spruce is susceptible to windthrow, especially after any kind of initial cutting in old-growth forests (fig. 11). Partial cutting increases the risk because the entire stand is opened up and therefore vulnerable. Windfall is usually less around clearcuts because only the boundaries between cut and leave areas are vulnerable, but losses can be substantial if no special effort is made to locate windfirm cutting unit boundaries (Alexander 1964, 1967). While the tendency of spruce to windthrow is usually attributed to a shallow

root system, the development of the root system varies with soil and stand conditions. Trees that have developed together in dense stands over long periods of time mutually protect each other and do not have the roots, boles, or crowns to withstand sudden exposure to wind if opened up too drastically. If the roots and boles are defective, the risk of windthrow is increased. Furthermore, regardless of the kind or intensity of cutting, or soil and stand conditions, windthrow is greater on some exposures than others. Alexander (1974) has identified spruce windfall risk in relation to exposures in Colorado as follows:

Below Average

1. Valley bottoms, except where parallel to the direction of prevailing winds, and flat areas.
2. All lower, and gentle, middle north- and east-facing slopes.
3. All lower, and gentle, middle south- and west-facing slopes that are protected from the wind by considerably higher ground not far to windward.

Above Average

1. Valley bottoms parallel to the direction of prevailing winds.



Figure 8.—Clearcutting old-growth spruce-fir in alternate strips on the Fraser Experimental Forest, Colorado.

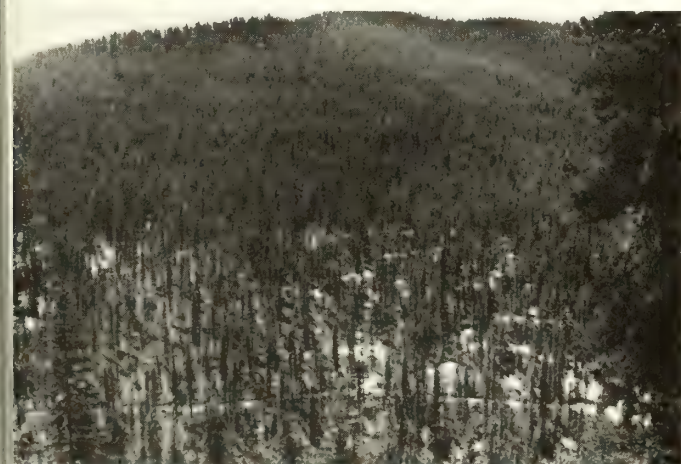


Figure 9.—First cut of a two-step shelterwood in old-growth spruce-fir on the Fraser Experimental Forest, Colorado.



Figure 10.—Group selection cutting in old-growth spruce-fir on the Fraser Experimental Forest, Colorado.



Figure 11.—Windthrown Engelmann spruce, Fraser Experimental Forest, Colorado.

2. Gentle, middle south and west slopes not protected to the windward.
3. Moderate to steep middle, and all upper north- and east-facing slopes.
4. Moderate to steep middle south- and west-facing slopes protected by considerably higher ground not far to windward.

Very High

1. Ridgetops.
2. Saddles in ridges.
3. Moderate to steep middle south- and west-facing slopes not protected to the windward.
4. All upper south- and west-facing slopes.

The risk of windfall is increased at least one category by such factors as poor drainage, shallow soils, defective roots and boles, and overly dense stands. Conversely, the risk of windfall is reduced if the stand is open-grown or composed of young, vigorous, sound trees. All situations become very high risk if exposed to special topographic situations such as gaps or saddles in ridges at higher elevations to the windward that can funnel winds into the area (Alexander 1964, 1967, 1974).

Insects.—The spruce beetle (*Dendroctonus rufipennis* Kirby) is the most serious insect pest of Engelmann spruce (Schmid and Frye 1977). It is restricted largely to mature and overmature spruce, and epidemics have occurred throughout recorded history. One of the most damaging recorded outbreaks was in Colorado from 1939 to 1951, when beetles killed nearly 4 billion board feet of standing spruce (Massey and Wygant 1954). Outbreaks have been largely associated with extensive windthrow, where down trees have provided an ample food supply needed for a rapid buildup of beetle populations. Cull material left after logging has also started outbreaks, and there are examples of heavy spruce beetle populations developing in scattered trees wind-thrown after heavy partial cutting. The beetle progeny then emerge to attack living trees, sometimes seriously damaging the residual stand. Occasionally, heavy spruce beetle outbreaks have developed in overmature stands with no recent history of cutting or windfall, but losses in uncut stands that have not been subjected to catastrophic wind storms have usually been no greater than normal mortality in old growth (Alexander 1974). Engelmann spruce is attacked by other insects, but only the defoliating western spruce budworm (*Choristoneura occidentalis* Freeman) is potentially dangerous (Furniss and Carolin 1977).

Diseases.—The most common diseases of Engelmann spruce are caused by wood-rotting fungi that result in loss of volume and predispose trees to windthrow and windbreak (Hinds and Hawksworth 1966). In a recent study of cull indicators and associated decay in Colorado, the major root and butt fungi in mature to overmature Engelmann spruce were identified as *Phellinus nigrolimitatus* (Rohm.) Bourd. et Galz., *Flammula alnicola* (Fr.) Kummer, *Polyporus tomentosus* var. *circnatus* (Fr.) Sartory et. Maire, *Gloeocystidiellum radiosum* (Fr.) Bord., and *Coniophora puteana* (Schum. ex Fr.) Karst. Trunk rots, which caused 88% of the decay, were associated with *Phellinus pini* (Thore ex Fr.) Pilat, *Haematosterceum sanguinolentum* (Alb. ex Schw. ex Fr.) Pouz., *Echinodontium sulcatum* (Burt) Gross, and *Amylosterceum chailletii* (Pers ex Fr.) Boid. Spruce broom rust (*Chrysomyxa arctostaphyli* Diet.) is also common in spruce-fir forests. It causes bole deformation, loss of volume, and spiketops; increases susceptibility to windbreak; and provides infection courts for decay fungi in spruce (Alexander 1958, 1965, Hinds and Hawksworth 1966). Dwarfmistletoe (*Arceuthobium microcarpum* (Engelm.) Hawk. and Wiens) causes heavy mortality in spruce in Arizona and New Mexico, but it has a limited range in the Southwest and is not found in the central Rocky Mountains (Hawksworth and Wiens 1972).

Fire.—Thin bark and persistence of dead lower limbs make Engelmann spruce susceptible to destruction or severe injury by fire. Many root and trunk rots in old growth appear to be associated with fire injury. Because of the climate where spruce grows, the risk of fire is less than in warmer and drier climates (Alexander 1958, 1965).

PROPERTIES AND USES OF THE WOOD

Engelmann spruce is one of the lightest of the important commercial woods in the United States. The wood is generally straight grained, has moderately small shrinkage, can be readily air-dried, and is a uniform color (McSwain et al. 1970). It is rated low in beam and post strength and in shock resistance. The wood is soft and machines well for ordinary uses. It has good nail-holding properties, glues well, and is easy to work, but paint-holding properties are only average. If sufficient time is allowed, the lumber can be kiln-dried without difficulty. The heartwood and sapwood are not durable when used under conditions favorable to decay. Spruce is considered somewhat resistant to preservative treatment; however, crossties have been successfully pressure-treated for many years (Anderson 1956).

The lumber of spruce is likely to contain many small knots. Consequently, it yields only minor amounts of select grades of lumber, but a relatively high proportion in the common grades (Mueller and Barger 1963). In the past, spruce was used principally for mine timbers, railroad ties, and poles. Today much of the lumber of spruce is used in home construction where high strength is not required and for prefabricated wood products. In recent years, rotary-cut spruce veneer has been used in plywood manufacture. Other uses of spruce include specialty items such as violins and pianos and in aircraft construction (McSwain et al. 1970). Spruce has not been used much for pulp and paper, but its pulping properties are excellent. Long fibers, light color, and absence of resins permit it to be pulped readily by the sulfite, sulfate, or groundwood processes (Anderson 1956).

GENETICS

Population Differences

Available information on population differences of Engelmann spruce is limited to relatively few studies. For example, spruce from high elevation seed sources and northern latitudes break dormancy first in the spring and are the first to become dormant in the fall when grown in low elevation nurseries with low and middle elevation seed sources. Conversely, low elevation and southern latitude seed sources frequently are more resistant to spring frosts, but are less winterhardy than middle and high elevation seed sources (Fowler and Roche 1977). In one study that compared seedlings from 20 seed sources, ranging from British Columbia to New Mexico, planted at an elevation of 9,600 feet in Colorado, seedlings from northern latitudes and lower elevations made the best height growth (Shepperd et al. 1981). Overall survival from all sources was 73%, with no significant differences between sources.

Races and Hybrids

There are no recognized races or geographical varieties of Engelmann spruce (Little 1979). There is

abundant evidence that natural introgressive hybridization between Engelmann and white spruce occurs in sympatric areas, especially around Glacier Park in Montana (Daubenmire 1974). It has been suggested that Engelmann and Sitka spruces (*Picea sitchensis* (Bong.) Carr) cross in British Columbia, but it seems more likely that the crosses are between Sitka and white spruce. Engelmann spruce has been artificially crossed with several other spruces, but with only limited success (Fowler and Roche 1977).

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APPENDIX

Habitat types, community types and plant communities in which *Picea engelmannii* is a major climax, co-climax, minor climax, or major seral

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Picea engelmannii</i> series						
<i>Picea engelmannii</i> / <i>Acer glabrum</i> H.T.	Chiricahua Mountains, Arizona; Sacramento Mountains, New Mexico	Warm moist	Climax	<i>Abies Lasiocarpa</i> <i>Pseudotsuga</i> <i>menziesii</i> <i>Populus</i> <i>tremuloides</i>	<i>A. glabrum</i> <i>Bromus ciliatus</i> <i>Viola canadensis</i> <i>Smilacina stellata</i>	Alexander et al. 1984a Moir and Ludwig 1979
<i>Picea engelmannii</i> / <i>Juniperus communis</i> H.T.	Wind River and Absaroka Mountains, northwestern Wyoming	Warm dry	Climax	<i>Pinus flexilis</i> <i>P. menziesii</i> <i>Pinus albicaulis</i> <i>Pinus contorta</i>	<i>J. communis</i> <i>Arnica cordifolia</i> <i>Frasera speciosa</i>	Steele et al. 1983
<i>Picea engelmannii</i> / <i>Linnaea borealis</i> H.T.	Mountains of Montana east of Continental Divide; Wind River Moun- tains, northwestern Wyoming	Cool well- drained	Climax	<i>P. contorta</i> <i>P. menziesii</i>	<i>L. borealis</i> <i>Vaccinium globulare</i> <i>Symphoricarpos albus</i> <i>J. communis</i>	Pfister et al. 1977 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Physocarpus malvaceus</i> H.T.	Mountains of south-central Montana, eastern Idaho, and north- western Wyoming	Warm moist	Climax	<i>A. lasiocarpa</i> (minor climax) <i>P. contorta</i> <i>P. menziesii</i>	<i>P. malvaceus</i> <i>Galium triflorum</i> <i>S. albus</i> <i>Spiraea betulifolia</i>	Pfister et al. 1977 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Ribes montigenum</i> H.T.	Wind River Mountains, north- western Wyoming; mountains of southern Utah	Cool dry to well-drained	Climax	<i>P. contorta</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. tremuloides</i>	<i>R. montigenum</i> <i>Aquilegia caerulea</i> <i>Sibbaldia procumbens</i> <i>Arnica latifolia</i> <i>Astragalus miser</i>	Pfister 1972 Steele et al. 1983 Youngblood 1984 ¹
<i>Picea engelmannii</i> / <i>Vaccinium caespitosum</i> H.T.	Mountains of northwestern Montana and northern Utah	Cool well- drained	Climax	<i>Larix occidentalis</i> <i>Pinus ponderosa</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>V. caespitosum</i> <i>L. borealis</i> <i>Vaccinium scoparium</i> <i>Calamagrostis</i> <i>rubescens</i> <i>R. montigenum</i>	Mauk and Henderson 1984 Pfister et al. 1977
<i>Picea engelmannii</i> / <i>Vaccinium myrtillus</i> H.T. <i>P. engelmannii</i> / <i>V. myrtillus</i> - <i>Polemonium pulcherrimum</i> H.T. [<i>P. engelmannii</i> / <i>V. scoparium</i> - <i>P. delicatum</i> H.T.]	Mountains of southern Colorado and northern New Mexico	Cool dry	Climax	<i>A. lasiocarpa</i> (minor climax) <i>WR Mts</i> <i>Pinus aristata</i> <i>P. tremuloides</i>	<i>P. delicatum</i> (<i>P. pulcherrimum</i>) <i>Senecio</i> spp. <i>Deschampsia</i> <i>caespitosa</i> <i>Poa reflexa</i>	DeVelice et al. 1984 ² Fitzhugh et al. 1984 ³ Moir and Ludwig 1979
<i>Picea engelmannii</i> / <i>Vaccinium scoparium</i> H.T.	Wind River and Bighorn Mountains, Wyoming; mountains of northern Utah	Cool dry	Climax	<i>A. lasiocarpa</i> (minor climax) <i>WR Mts</i> <i>P. flexilis</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. albicaulis</i>	<i>V. scoparium</i> <i>A. cordifolia</i> <i>Carex rossii</i> <i>Antennaria</i> spp. <i>Fragaria virginiana</i>	Hoffman and Alexander 1976 Mauk and Henderson 1984 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Bromus ciliatus</i> H.T.	Mogollon and Black Mountains, New Mexico	Cool dry	Climax	<i>P. menziesii</i>	<i>B. ciliatus</i> <i>C. rossii</i> <i>A. miser</i> <i>Fragaria</i> spp.	Fitzhugh et al. 1984 ³
<i>Picea engelmannii</i> / <i>Elymus triticoides</i> H.T.	Capitan Mountains, New Mexico	Cool dry to well- drained	Climax or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i>	<i>E. triticoides</i> <i>A. glabrum</i> <i>Jamesia americana</i>	Alexander et al. 1984a Moir and Ludwig 1979

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Picea engelmannii</i> / <i>Carex disperma</i> H.T.	Mountains of central and southern Idaho, and northwestern Wyoming	Cool moist	Climax	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>Picea pungens</i>	<i>C. disperma</i> <i>Pyrola secunda</i> <i>G. triflorum</i>	Steele et al. 1981 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Carex foenea</i> H.T.	Pinaleno Mountains, Arizona	Cool dry	Climax	Generally in pure stands	<i>C. foenea</i>	Moir and Ludwig 1979
<i>Picea engelmannii</i> / <i>Arnica cordifolia</i> H.T.	Mountains of northwestern Wyoming	Cool well- drained	Climax	<i>P. menziesii</i> <i>P. flexilis</i> <i>P. albicaulis</i> <i>P. tremuloides</i>	<i>A. cordifolia</i> <i>C. rossii</i> <i>A. miser</i> <i>F. speciosa</i>	Steele et al. 1983
<i>Picea engelmannii</i> / <i>Caltha leptosepala</i> H.T.	Uinta Mountains, Utah; mountains of northwestern Wyoming and Idaho	Cool moist	Climax	<i>A. lasiocarpa</i> <i>P. contorta</i>	<i>C. leptosepala</i> <i>V. scoparium</i> <i>D. caespitosa</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northwestern Montana	Warm moist to dry	Climax	<i>P. contorta</i> <i>P. ponderosa</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>C. uniflora</i> <i>V. caespitosum</i> <i>Aralia nudicaulis</i> <i>Cornus canadensis</i>	Pfister et al. 1977
<i>Picea engelmannii</i> / <i>Equisetum arvense</i> H.T.	Mountains of north- central Washington, Montana, central Idaho, northwestern Wyoming, and northern Utah	Warm to cool wet	Climax	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. pungens</i>	<i>E. arvense</i> <i>Equisetum seirpoides</i> <i>Streptopus</i> <i>amplexifolius</i> <i>Senecio triangularis</i> <i>Luzula parviflora</i>	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Williams and Lillybridge 1983
<i>Picea engelmannii</i> / <i>Galium triflorum</i> H.T.	Mountains of south-central Montana, central Idaho, and north- western Wyoming	Warm moist	Climax	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. pungens</i> <i>P. ponderosa</i> <i>P. menziesii</i>	<i>G. triflorum</i> <i>Actaea rubra</i> <i>S. stellata</i> <i>S. amplexifolius</i>	Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Geum rossii</i> H.T.	San Francisco Peaks, Arizona	Cool dry	Climax	<i>P. tremuloides</i>	<i>G. rossii</i> <i>P. delicatum</i> <i>Festuca brachyphylla</i>	Moir and Ludwig 1979
<i>Picea engelmannii</i> / <i>Hypnum revolutum</i> H.T.	Mountains of southeastern Idaho and north- western Wyoming	Cool dry	Climax	<i>P. flexilis</i> <i>P. albicaulis</i> <i>P. menziesii</i>	<i>H. revolutum</i> <i>Discranowiesia</i> <i>crispula</i>	Steele et al. 1981 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Senecio cardamine</i> H.T.	Blue Mountains, Arizona	Cool moist	Climax	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>Pinus strobiformis</i> <i>Abies concolor</i> <i>P. tremuloides</i>	<i>S. cardamine</i> <i>Geranium richardsonii</i> <i>Fragaria ovalis</i> <i>V. canadensis</i>	Fitzhugh et al. 1984 ³
<i>Picea engelmannii</i> / <i>Senecio streptanthifolius</i> H.T.	Mountains of central and southwestern Montana	Cool dry to well-drained	Climax	<i>P. flexilis</i> <i>P. albicaulis</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>S. streptanthifolius</i> <i>P. secunda</i> <i>A. cordifolia</i>	Pfister et al. 1977
<i>Picea engelmannii</i> / <i>Smilacina stellata</i> H.T.	Mountains of Montana east of Continental Divide	Warm moist	Climax	<i>P. contorta</i> <i>P. ponderosa</i> <i>P. menziesii</i>	<i>S. stellata</i> <i>Smilacina racemosa</i> <i>Thalictrum occidentale</i>	Pfister et al. 1977

APPENDIX—Continued

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Picea engelmannii</i> / <i>Trifolium dasyphyllum</i> H.T.	High mountains of central Colorado	Cold dry	Climax or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. flexilis</i>	<i>T. dasyphyllum</i> <i>Pyrola chlorantha</i> <i>Sedum lanceolatum</i> <i>Trisetum spicatum</i>	Hess 1981
<i>Picea engelmannii</i> / Moss spp. H.T.	Mountains of New Mexico and Arizona	Cool moist to well- drained	Climax or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. aristata</i> <i>P. menziesii</i>	Moss spp. <i>Ribes</i> spp. <i>Lathyrus arizonicus</i> <i>Vaccinium</i> spp. <i>Rosa</i> spp.	Alexander et al. 1984b ⁴ Fitzhugh et al. 1984 ³ Moir and Ludwig 1979
<i>Picea engelmannii</i> / Bottomlands P.C.	Mountains of central Oregon	Warm moist	Long-lived seral to <i>Abies amabilis</i>	<i>A. amabilis</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. ponderosa</i>	<i>L. borealis</i> <i>Rubus ursinus</i>	Volland 1976
<i>Picea engelmannii</i> / Scree H.T.	Mountains of northern New Mexico and southern Colorado	Warm dry	Climax	<i>A. lasiocarpa</i> (minor climax)	<i>J. communis</i> <i>Saxifraga</i> <i>bronchialis</i>	DeVelice et al. 1984 ²
<i>Abies lasiocarpa</i> series						
<i>Abies lasiocarpa</i> / <i>Acer glabrum</i> H.T.	Mountains of of central and southern Idaho, northern and central Utah, and northwestern Wyoming; mountains of northern New Mexico	Warm moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. pungens</i> <i>A. concolor</i>	<i>A. glabrum</i> <i>T. occidentale</i> <i>Thalictrum fendleri</i> <i>Osmorhiza chilensis</i> <i>A. cordifolia</i>	Alexander et al. 1984b ⁴ Mauk and Henderson 1984 Steele et al. 1981 Steele et al. 1983 Youngblood 1984 ¹
<i>Abies lasiocarpa</i> / <i>Alnus sinuata</i> H.T.	Mountains of central Idaho and central and south- western Montana	Cool moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>L. occidentalis</i>	<i>A. sinuata</i> <i>V. scoparium</i> <i>Xerophyllum tenax</i> <i>V. globulare</i>	Pfister et al. 1977 Steele et al. 1981
<i>Abies lasiocarpa</i> / <i>Berberis repens</i> H.T.	Mountains of Utah, north- western Wyoming, and southeastern Idaho	Warm to cool, well- drained	Minor climax to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. pungens</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. flexilis</i> <i>A. concolor</i> <i>P. tremuloides</i>	<i>B. repens</i> <i>R. montigenum</i> <i>Carex geyeri</i> <i>Pachistima myrsinites</i> <i>Symphoricarpos</i> <i>oreophilus</i>	Mauk and Henderson 1984 Pfister 1972 Steele et al. 1983 Youngblood 1984 ¹
<i>Abies lasiocarpa</i> / <i>Clematis pseudoalpina</i> H.T.	Mountains of Montana east of Continental Divide	Warm dry	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. flexilis</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>C. pseudoalpina</i> <i>Clematis tenuiloba</i>	Pfister et al. 1977
<i>Abies lasiocarpa</i> / <i>Juniperus communis</i> H.T.	Mountains of central Idaho, northwestern Wyoming, Utah, northern Arizona, and New Mexico	Warm to cold dry	Seral to or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>A. concolor</i> (AZ, NM only) <i>P. pungens</i> (UT)	<i>J. communis</i> <i>P. secunda</i> <i>Shepherdia</i> <i>canadensis</i> <i>V. globulare</i> <i>Rosa woodsii</i> <i>S. oreophilus</i>	Mauk and Henderson 1984 Moir and Ludwig 1979 Steele et al. 1981 Steele et al. 1983 Youngblood 1984 ¹

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority'
<i>Abies lasiocarpa</i> / <i>Linnaea borealis</i> H.T. <i>A. lasiocarpa</i> - <i>Picea engelmannii</i> IL. <i>borealis</i> P.C.	Mountains of north-central Washington, Montana, central and southern Idaho, northwestern Wyoming and central Colorado	Cool, moist to well-drained	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>A. concolor</i> <i>L. occidentalis</i>	<i>L. borealis</i> <i>A. cordifolia</i> <i>V. scoparium</i> <i>C. rubescens</i> <i>Rubus parviflorus</i>	Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ⁵ Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Menziesia ferruginea</i> H.T.	Mountains of southeastern Washington, eastern Oregon, Montana, Idaho, and northwestern Wyoming	Cool moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>Pinus monticola</i> <i>L. occidentalis</i>	<i>M. ferruginea</i> <i>V. globulare</i> <i>Rhododendron albiflorum</i> <i>Ledum glandulosum</i> <i>A. latifolia</i> <i>X. tenax</i>	Cooper et al. 1983 ⁸ Daubenmire and Daubenmire 1968 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Oplopanax horridum</i> H.T.	Mountains of northern to wet Montana	Cool moist	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. monticola</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>O. horridum</i> <i>Taxus brevifolia</i>	Pfister et al. 1977
<i>Abies lasiocarpa</i> / <i>Pachistima myrsinites</i> H.T. <i>A. lasiocarpa</i> - <i>Picea engelmannii</i> IP. <i>myrsinites</i> P.C.	Mountains of southern British Columbia and north-central Washington; Rocky Mountains of Canada south to southern Colorado	Warm dry to well-drained	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. monticola</i> <i>P. tremuloides</i> <i>L. occidentalis</i>	<i>P. myrsinites</i> <i>C. uniflora</i> <i>G. triflorum</i> <i>C. geyeri</i> <i>Erigeron</i> spp.	Daubenmire and Daubenmire 1968 Hess and Wasser 1982 ⁸ McLean 1970 Steen and Dix 1974 ⁵ Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Phyllodoce empritiformis</i> P.C.	Eastside Cascades, north-central Washington	Cool moist	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. albicaulis</i>	<i>P. empritiformis</i> <i>V. scoparium</i>	Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Physocarpus malvaceus</i> H.T.	Mountains of eastern Idaho, northwestern Wyoming, and northern and central Utah	Warm moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>P. malvaceus</i> <i>A. cordifolia</i> <i>Amelanchier alnifolia</i> <i>Sorbus scopulina</i> <i>A. glabrum</i> <i>S. canadensis</i>	Mauk and Henderson 1984 Steele et al. 1983 Youngblood 1984'
<i>Abies lasiocarpa</i> / <i>Rhododendron albiflorum</i> P.C.	Eastside Cascades, north-central Washington	Cool moist	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>R. albiflorum</i> <i>L. glandulosum</i>	Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Ribes montigenum</i> H.T.	Mountains of southern Montana, Idaho, Utah, and northwestern Wyoming	Cool dry	Seral to or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>R. montigenum</i> <i>A. latifolia</i> <i>T. fendleri</i> <i>Antennaria microphylla</i> <i>Mertensia arizonica</i>	Mauk and Henderson 1984 Pfister 1972 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Youngblood 1984'

APPENDIX—Continued

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Rubus parviflorus</i> H.T.	Mimbres and Mogollon Mountains, New Mexico; San Juan Mountains, Colorado	Cool moist	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>A. concolor</i> <i>P. tremuloides</i>	<i>R. parviflorus</i> <i>Vaccinium myrtillus</i> <i>A. glabrum</i>	DeVelice et al. 1984 ² Fitzhugh et al. 1984 ³ Moir and Ludwig 1979
<i>Abies lasiocarpa</i> / <i>Salix glauca</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>S. glauca</i> H.T.	High mountains of Colorado	Cold wet	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. flexilis</i>	<i>S. glauca</i> <i>V. myrtillus</i> <i>P. pulcherrimum</i> <i>Acomastylis rossii</i>	Hess 1981 Hess and Wasser 1982 ⁶ Komarkova 1984 ⁸
<i>Abies lasiocarpa</i> / <i>Shepherdia canadensis</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>S. canadensis</i> P.C.	Bighorn Mountains, north-central Wyoming; mountains of north-central Colorado	Cool to warm dry	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>S. canadensis</i> <i>V. scoparium</i>	Hoffman and Alexander 1976 Steen and Dix 1974 ⁵
<i>Abies lasiocarpa</i> / <i>Spiraea betulifolia</i> H.T.	Mountains of central and southern Idaho, and northwestern Wyoming	Warm dry	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. albicaulis</i>	<i>S. betulifolia</i> <i>C. geyeri</i> <i>C. rubescens</i> <i>P. myrsinites</i>	Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Symphoricarpos albus</i> H.T.	Mountains of southeastern Idaho and north- western Wyoming	Warm well- drained	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>S. albus</i> <i>A. alnifolia</i> <i>C. rubescens</i>	Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Vaccinium caespitosum</i> H.T.	Mountains of south central Montana, central Idaho, and northern and central Utah	Cool well- drained	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>V. caespitosum</i> <i>L. borealis</i> <i>C. rubescens</i> <i>V. scoparium</i> <i>A. cordifolia</i>	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Youngblood 1984 ¹
<i>Abies lasiocarpa</i> / <i>Vaccinium globulare</i> H.T.	Mountains of Montana, central and southern Idaho, northern Utah, and northwestern Wyoming	Cool well- drained	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>V. globulare</i> <i>P. myrsinites</i> <i>Lonicera utahensis</i> <i>A. cordifolia</i>	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Vaccinium membranaceum</i> H.T.	Blue Mountains, Washington and Oregon; mountains of central Utah	Warm dry to well- drained	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>L. occidentalis</i>	<i>V. membranaceum</i> <i>P. myrsinites</i> <i>A. cordifolia</i> <i>C. rossii</i>	Hall 1973 Youngblood 1984 ¹
<i>Abies lasiocarpa</i> / <i>Vaccinium myrtillus</i> H.T. [<i>A. lasiocarpa</i> / <i>V. myrtillus</i> - <i>Linnaea borealis</i> H.T.] [<i>A. lasiocarpa</i> / <i>V. myrtillus</i> - <i>Rubus parviflorus</i> H.T.] [<i>A. lasiocarpa</i> / <i>Vaccinium</i> <i>scoparium</i> - <i>L. borealis</i> H.T.]	Mountains of eastern Arizona, northern New Mexico, and southern Colorado; La Sal mountains, Utah	Cool well- drained	Climax or co-climax with <i>A. lasiocarpa</i> (AZ)	<i>A. lasiocarpa</i> <i>A. concolor</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>P. aristata</i> <i>P. flexilis</i>	<i>V. myrtillus</i> <i>V. scoparium</i> <i>Lonicera involucrata</i> <i>P. myrsinites</i> <i>A. cordifolia</i> <i>R. montigenum</i> <i>L. borealis</i> <i>R. parviflorus</i>	Alexander et al. 1984b ⁴ DeVelice et al. 1984 ² Fitzhugh et al. 1984 ³ Moir and Ludwig 1979 Youngblood 1984 ¹

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Vaccinium scoparium</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> IV. <i>scoparium</i> H.T.; P.C. [<i>P. engelmannii</i> IV. <i>scoparium</i> H.T.]	Mountains of British Columbia and Alberta south to Arizona and New Mexico; mountains of eastern and north- central Washington and eastern Oregon	Cool dry	Climax, co-climax with, or minor climax to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>L. occidentalis</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. pungens</i> <i>A. concolor</i>	<i>V. scoparium</i> <i>C. rubescens</i> <i>V. myrtillus</i> <i>A. cordifolia</i> <i>C. geyeri</i> <i>Erigeron superbus</i> (<i>E. eximius</i>) <i>L. borealis</i> <i>P. myrsinites</i> <i>P. empetriflorum</i>	Daubenmire and Daubenmire 1968 Hall 1973 Hess 1981 Hess and Wasser 1982 ⁷ Hoffman and Alexander 1980 Hoffman and Alexander 1980 Hoffman and Alexander 1983 Komarkova 1984 ⁸ McLean 1970 Mauk and Henderson 1984 Pfister 1972 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ⁵ Williams and Lillybridge 1983 Wirsing and Alexander 1975
<i>Abies lasiocarpa</i> - <i>Pinus albicaulis</i> / <i>Vaccinium scoparium</i> H.T.	Mountains of of Montana east of Continental Divide	Cool dry	Seral to <i>A. lasiocarpa</i> <i>P. albicaulis</i>	<i>A. lasiocarpa</i> <i>P. albicaulis</i> <i>P. contorta</i>	<i>V. scoparium</i> <i>C. geyeri</i> <i>X. tenax</i> <i>A. latifolia</i>	Pfister et al. 1977
<i>Abies lasiocarpa</i> / <i>Vaccinium</i> spp. P.C.	Eastside Cascades, north-central Washington	Cool dry	Co-climax with <i>A. lasiocarpa</i> <i>P. menziesii</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>L. occidentalis</i>	<i>Vaccinium</i> spp. <i>C. rossii</i> <i>P. myrsinites</i> <i>Arctostaphylos</i> <i>uva-ursi</i>	Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Xerophyllum tenax</i> H.T.	Mountains of of northern Idaho, eastern Washington and Oregon, Idaho, Montana, and northwestern Wyoming	Warm dry	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. albicaulis</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>X. tenax</i> <i>V. membranaceum</i> <i>V. scoparium</i> <i>V. globulare</i> <i>Luzula hitchcockii</i>	Cooper et al. 1983 ⁸ Daubenmire and Daubenmire 1968 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Calamagrostis canadensis</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> IC. <i>canadensis</i> H.T. [<i>P. engelmannii</i> IC. <i>canadensis</i> H.T.]	Mountains of central Montana, Idaho, north- western Wyoming, and northern Utah; mountains of north-central and western Colorado	Cool wet	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>C. canadensis</i> <i>V. caespitosum</i> <i>L. glandulosum</i> <i>S. triangularis</i> <i>G. triflorum</i>	Cooper et al. 1983 ⁸ Hess 1981 Komarkova 1984 ⁸ Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983

APPENDIX—Continued

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Calamagrostis rubescens</i> H.T.	Mountains of north- central Washington, Montana east of Continental Divide, central and southern Idaho, northern Utah, and northwestern Wyoming	Warm dry	Co-climax with or seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>L. occidentalis</i>	<i>C. rubescens</i> <i>O. chilensis</i> <i>T. occidentale</i> <i>C. geyeri</i> <i>A. cordifolia</i> <i>P. myrsinites</i>	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Luzula hitchcockii</i> H.T.	Mountains of Montana west of Continental Divide, Idaho, and northwestern Wyoming	Cool well- drained	Minor climax or seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. albicaulis</i>	<i>L. hitchcockii</i> <i>A. latifolia</i> <i>X. tenax</i> <i>A. cordifolia</i> <i>V. scoparium</i> <i>M. ferruginea</i>	Cooper et al. 1983 ^a Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Carex</i> <i>geyeri</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> - <i>C. geyeri</i> H.T.; P.C. [<i>P. engelmannii</i> / <i>C. geyeri</i> H.T.]	Mountains of Montana, central Idaho, southern Utah, Wyoming, and north-central and western Colorado	Cool dry to warm dry	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. albicaulis</i> <i>P. tremuloides</i>	<i>C. geyeri</i> <i>A. cordifolia</i> <i>S. oreophilus</i> <i>Lupinus argenteus</i> <i>B. repens</i> <i>Lathyrus lanszwertii</i>	Hess 1981 Hess and Wasser 1981 ^a Hoffman and Alexander 1980 Hoffman and Alexander 1983 Komarkova 1984 ^a Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ^a Wirsing and Alexander 1975 Youngblood 1984 ¹
<i>Abies lasiocarpa</i> / <i>Carex rossii</i> H.T.	Mountains of central and southern Utah	Cool dry	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>C. rossii</i> <i>A. cordifolia</i> <i>A. miser</i> <i>R. woodsii</i>	Youngblood 1984 ¹
<i>Abies lasiocarpa</i> / <i>Aconitum columbianum</i> H.T.	Mountains of central and southern Utah	Cool moist	Seral to or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>A. concolor</i>	<i>A. columbianum</i> <i>A. rubra</i> <i>A. cordifolia</i> <i>B. ciliatus</i>	Youngblood 1984 ¹
<i>Abies lasiocarpa</i> / <i>Actaea rubra</i> H.T.	Mountains of central Idaho northern Utah, and northwestern Wyoming	Warm moist lower slopes	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. pungens</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>A. rubra</i> <i>O. chilensis</i> <i>L. utahensis</i> <i>V. globulare</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Arnica cordifolia</i> H.T.	Mountains of Montana east of Continental Divide, central Idaho, northwestern and north-central Wyoming, and western Colorado	Cool well- drained	Seral to or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. albicaulis</i>	<i>A. cordifolia</i> <i>P. secunda</i> <i>A. miser</i> <i>F. virginiana</i> <i>P. tremuloides</i>	Hoffman and Alexander 1976 Komarkova 1984 ^a Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Arnica latifolia</i> H.T.	Mountains of southern Idaho, northern Utah, and northwestern Wyoming	Cool dry	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>P. albicaulis</i>	<i>A. latifolia</i> <i>Aster engelmannii</i> <i>Pedicularis racemosa</i>	Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Caltha biflora</i> H.T.	Mountains of central Idaho	Cool wet	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i>	<i>C. biflora</i> <i>L. involucreta</i> <i>Pedicularis bracteosa</i> <i>Dodecatheon jeffreyi</i>	Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> / <i>Cardamine cordifolia</i> P.C. [<i>A. lasiocarpa</i> / <i>Mertensia ciliata</i> H.T.]	Mountains of north-central and southern Colorado	Cool wet	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i>	<i>C. cordifolia</i> <i>M. ciliata</i> <i>Mitella pentandra</i> <i>Carex bella</i>	DeVelice et al. 1984 ² Steen and Dix 1974 ⁵
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northwestern Montana, and central and northern Idaho	Warm moist to dry	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. monticola</i>	<i>C. uniflora</i> <i>M. ferruginea</i> <i>V. caespitosum</i> <i>A. nudicaulis</i> <i>X. tenax</i>	Cooper et al. 1983 ⁶ Pfister et al. 1977 Steele et al. 1981
<i>Abies lasiocarpa</i> / <i>Coptis occidentalis</i> H.T.	Mountains of central and northern Idaho	Warm moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. contorta</i>	<i>C. occidentalis</i> <i>X. tenax</i> <i>V. globulare</i> <i>M. ferruginea</i>	Cooper et al. 1983 ⁶ Steele et al. 1981
<i>Abies lasiocarpa</i> / <i>Erigeron superbus</i> (<i>E. eximius</i>) H.T.	Mountains of southwestern Colorado, northern New Mexico, and Arizona	Cool dry	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. ponderosa</i> <i>A. concolor</i> <i>P. menziesii</i> <i>P. strobiformis</i> <i>P. tremuloides</i>	<i>E. superbus</i> (<i>E. eximius</i>) <i>G. richardsonii</i> <i>L. arizonicus</i> <i>L. involucreta</i> <i>A. cordifolia</i>	Alexander et al. 1984b ⁴ DeVelice et al. 1984 ² Fitzhugh et al. 1984 ³ Moir and Ludwig 1979
<i>Abies lasiocarpa</i> / <i>Galium triflorum</i> H.T.	Mountains of Montana	Warm moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>G. triflorum</i> <i>A. rubra</i> <i>S. amplexifolius</i>	Pfister et al. 1977
<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> / <i>Lupinus argenteus</i> P.C.	Mountains of central and southern Colorado	Warm well- drained	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i>	<i>L. argenteus</i> <i>V. scoparium</i>	Steen and Dix 1974 ⁵
<i>Abies lasiocarpa</i> / <i>Osmorhiza chilensis</i> H.T.	Mountains of southern Idaho and northern Utah	Warm moist to well- drained	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>O. chilensis</i> <i>C. rossii</i> <i>B. repens</i> <i>P. myrsinites</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Pedicularis racemosa</i> H.T.	Mountains of southeastern Idaho, north- western Wyoming, and northern Utah	Warm dry	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>P. racemosa</i> <i>A. cordifolia</i> <i>S. oreophilus</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Polenonium delicatum</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>P. delicatum</i> P.C.	Mountains of of central and western Colorado	Cool dry	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>P. delicatum</i> <i>Osmorhiza obtusa</i> <i>Vaccinium</i> sp.	Komarkova 1984 ⁸ Steen and Dix 1974 ⁵
<i>Abies lasiocarpa</i> / <i>Senecio sanguisorboides</i> H.T.	Sacramento Mountains, southern New Mexico.	Cool dry to well- drained	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>S. sanguisorboides</i> <i>R. montigenum</i> <i>Ribes wolfii</i>	Alexander, et al. 1984a Moir and Ludwig 1979

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> l <i>Senecio triangularis</i> H.T. [<i>P. engelmannii</i> l <i>S. triangularis</i> H.T.]	Mountains of central and western Colorado	Warm moist	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i>	<i>S. triangularis</i> <i>M. ciliata</i> <i>C. cordifolia</i> <i>E. arvense</i>	Hess 1981 Komarkova 1984 ^a
<i>Abies lasiocarpa</i> l <i>Streptopus amplexifolius</i> H.T.	Mountains of south- central Idaho and northwestern Utah	Warm to moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i>	<i>S. amplexifolius</i> <i>S. triangularis</i> <i>A. columbianum</i> <i>Liquisticum canbyi</i>	Cooper et al. 1984 ^a Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> l <i>Thalictrum occidentale</i> H.T.	Mountains of southeastern Idaho and northwestern Wyoming	Warm well- drained	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>T. occidentale</i> <i>A. cordifolia</i> <i>O. chilensis</i>	Steele et al. 1983
<i>Abies lasiocarpa</i> l Moss sp. H.T. <i>A. lasiocarpa</i> - <i>Picea engelmannii</i> l Moss spp. P.C.	Mountains of northern New Mexico, and central, western, and southwestern Colorado	Cool dry	Co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. aristata</i>	Moss spp. <i>V. caespitosum</i> <i>Rosa</i> spp.	DeVelice et al. 1984 ² Komarkova 1984 ^a Steen and Dix 1974 ⁵
<i>Picea pungens</i> series						
<i>Picea pungens</i> l <i>Linnaea borealis</i> H.T. [<i>P. pungens</i> - <i>Pseudotsuga menziesii</i> l <i>L. borealis</i> H.T.]	Sangre de Cristo Mountains, southern Colorado and northern New Mexico	Cool well- drained	Minor climax to <i>P. pungens</i> <i>P. menziesii</i>	<i>P. pungens</i> <i>P. menziesii</i> <i>A. concolor</i> <i>P. tremuloides</i>	<i>L. borealis</i> <i>P. myrsinites</i> <i>V. myrtilus</i>	DeVelice et al. 1984 ² Moir and Ludwig 1979
<i>Picea pungens</i> l <i>Carex foenea</i> H.T.	Mountains of northern New Mexico	Cool moist	Minor climax to <i>P. pungens</i> <i>P. menziesii</i>	<i>P. pungens</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>P. menziesii</i>	<i>C. foenea</i> <i>A. glabrum</i> <i>Festuca arizonica</i> <i>E. eximius</i>	Alexander et al. 1984b ⁴
<i>Picea pungens</i> l <i>Equisetum arvense</i> H.T.	Mountains of southern Utah	Warm to cool wet	Minor climax to <i>P. pungens</i>	<i>P. pungens</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>E. arvense</i> <i>G. richardsonii</i> <i>T. fendleri</i> <i>O. chilensis</i>	Youngblood 1984 ¹
<i>Picea pungens</i> l <i>Erigeron eximius</i> [<i>P. pungens</i> - <i>Picea engelmannii</i> l <i>E. superbus</i> H.T.]	Mountains of of northern New Mexico and southern Colorado	Cool dry	Minor climax to <i>P. pungens</i> <i>P. menziesii</i> <i>A. concolor</i>	<i>P. pungens</i> <i>P. menziesii</i> <i>A. concolor</i> <i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. strobiformis</i> <i>P. ponderosa</i> <i>P. flexilis</i>	<i>E. superbus</i> (<i>E. eximius</i>) <i>G. richardsonii</i> <i>T. fendleri</i> <i>F. arizonica</i> <i>C. foenea</i> <i>F. virginiana</i>	DeVelice et al. 1984 ² Fitzhugh et al. 1984 ³ Moir and Ludwig 1979
<i>Picea pungens</i> l <i>Fragaria ovalis</i> H.T.	Mountains of New Mexico	Cool moist	Minor climax <i>P. menziesii</i>	<i>P. pungens</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>P. strobiformis</i> <i>P. tremuloides</i> <i>A. concolor</i>	<i>F. ovalis</i> <i>C. foenea</i> <i>F. arizonica</i> <i>E. superbus</i> (<i>E. eximius</i>)	Alexander et al. 1984a Fitzhugh et al. 1984 ³
<i>Picea pungens</i> l <i>Senecio cardamine</i> H.T. [<i>P. pungens</i> - <i>Picea engelmannii</i> l <i>S. cardamine</i> H.T.]	White Mountains, Arizona	Cool moist	Co-climax with <i>P. pungens</i>	<i>P. pungens</i> <i>A. lasiocarpa</i> (minor climax) <i>P. menziesii</i> <i>A. concolor</i> <i>P. strobiformis</i> <i>P. tremuloides</i> <i>P. ponderosa</i>	<i>S. cardamine</i> <i>Pteridium aquilinum</i> <i>Helenium hoopesii</i> <i>V. canadensis</i>	Fitzhugh et al. 1984 ³ Moir and Ludwig 1979

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus contorta</i> series and other <i>P. contorta</i> dominated vegetation						
<i>Pinus contorta</i> l <i>Alnus crispa</i> P.C.	Mountains of Alberta and southern British Columbia	Cool moist to well- drained	Co-climax with <i>Picea glauca</i> <i>A. lasiocarpa</i>	<i>P. glauca</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>A. crispa</i> <i>C. canadensis</i> <i>A. uva-ursi</i> <i>L. borealis</i> <i>A. cordifolia</i> <i>Vaccinium</i> <i>myrtilloides</i>	Corns 1978 Corns and LaRoi 1976 LaRoi and Hnatiuk 1980 Wali and Krajina 1973
<i>Pinus contorta</i> l <i>Arctostaphylos uva-ursi</i> P.C. (CO); H.T. (UT)	Uinta Mountains Utah; mountains of north-central Colorado	Warm dry	Minor climax to <i>P. contorta</i> (UT); ultimate climax unknown (CO); probably seral to or co-climax with <i>A. lasiocarpa</i>	<i>P. contorta</i> <i>P. tremuloides</i> <i>A. lasiocarpa</i> <i>P. engelmannii</i>	<i>A. uva-ursi</i> <i>B. repens</i> <i>Sitanion hystrix</i>	Mauk and Henderson 1984 Steen and Dix 1974 ⁵
<i>Pinus contorta</i> l <i>Juniperus communis</i> H.T. (CO); C.T. (ID,WY)	Mountains of eastern Idaho and northwestern Wyoming; mountains of north-central Colorado	Warm dry	Minor climax to <i>P. contorta</i> (CO); ultimate climax unknown (ID, WY); probably seral to or co- climax with <i>A. lasiocarpa</i>	<i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>P. albicaulis</i> <i>A. lasiocarpa</i>	<i>J. communis</i> <i>A. uva-ursi</i> <i>S. canadensis</i> <i>A. cordifolia</i>	Hess 1981 Steele et al. 1983
<i>Pinus contorta</i> l <i>Ledum groenlandicum</i> P.C.	Mountains and foothills of Alberta	Cool moist	Co-climax with <i>P. glauca</i> <i>Picea mariana</i>	<i>P. contorta</i> <i>P. glauca</i> <i>P. mariana</i> <i>A. lasiocarpa</i> <i>P. menziesii</i>	<i>L. groenlandicum</i> <i>V. scoparium</i> <i>C. canadensis</i> <i>Pleurozium schreberi</i> <i>V. membranaceum</i>	Corns 1978 Corns and LaRoi 1976 LaRoi and Hnatiuk 1980
<i>Pinus contorta</i> l <i>Linnaea borealis</i> C.T. (MT,WY); P.C. (CO)	Mountains of Montana east of Continental Divide, north- western Wyoming, and central Colorado	Cool moist to well- drained	Ultimate climax unknown; probably seral to or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>L. borealis</i> <i>V. scoparium</i> <i>V. globulare</i> <i>A. cordifolia</i> <i>C. rubescens</i>	Pfister et al. 1977 Steele et al. 1983 Steen and Dix 1974 ⁵
<i>Pinus contorta</i> l <i>Menziesia glabella</i> P.C.	Mountains of Alberta	Cool moist	Co-climax with <i>P. glauca</i> <i>P. menziesii</i> <i>A. lasiocarpa</i>	<i>P. glauca</i> <i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>M. glabella</i> <i>V. scoparium</i> <i>Rubus pedatus</i> <i>L. borealis</i> <i>C. canadensis</i>	Corns 1978 LaRoi and Hnatiuk 1980
<i>Pinus contorta</i> l <i>Pachistima myrsinites</i> P.C.	Mountains of north-central Colorado	Warm dry to well-drained	Ultimate climax unknown; probably co- climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. contorta</i>	<i>P. myrsinites</i> <i>V. scoparium</i> <i>J. communis</i> <i>L. borealis</i> <i>Lathyrus leucanthus</i>	Steen and Dix 1974 ⁵
<i>Pinus contorta</i> l <i>Purshia tridentata</i> H.T.	Mountains of southern Washington, northern and central Oregon, and western Montana	Cool-warm dry to well- drained	Seral to <i>P. menziesii</i> or <i>A. lasiocarpa</i> where <i>P. con-</i> <i>torta</i> is not a topoedaphic climax	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>P. ponderosa</i> <i>P. contorta</i>	<i>P. tridentata</i> <i>A. uva-ursi</i> <i>C. rossii</i> <i>Ribes cereum</i> <i>Festuca idahoensis</i> <i>Epilobium</i> <i>angustifolium</i> <i>Stipa occidentalis</i> <i>Carex pensylvanica</i>	Pfister et al. 1977 Volland 1976 Youngberg and Dahms 1970
<i>Pinus contorta</i> l <i>Ribes viscosissimum</i> P.C.	Mountains of central Oregon	Cool dry	Seral to <i>Abies grandis</i> <i>Tsuga merten-</i> <i>siana</i>	<i>A. grandis</i> <i>T. mertensiana</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>R. viscosissimum</i> <i>Chimaphila umbellata</i> <i>Lupinus</i> spp.	Youngberg and Dahms 1970

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus contorta</i> l <i>Shepherdia canadensis</i> C.T.; P.C.	Mountains of southern British Columbia and Alberta, southeastern Idaho, northwestern Wyoming, and central Colorado	Cool-warm dry to well- drained	Ultimate climax unknown; probably co- climax with <i>P. glauca</i> , <i>A. menziesii</i> or <i>A. lasiocarpa</i>	<i>P. glauca</i> <i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>S. canadensis</i> <i>A. cordifolia</i> <i>J. communis</i> <i>L. borealis</i> <i>A. uva-ursi</i>	LaRoi and Hnatiuk 1980 Steen and Dix 1974 ⁵ Steele et al. 1983 Wali and Krajina 1973
<i>Pinus contorta</i> l <i>Spiraea betulifolia</i> C.T.	Mountains of eastern Idaho and northwestern Wyoming	Warm dry	Ultimate climax unknown; probably seral or minor climax to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>S. betulifolia</i> <i>C. rubescens</i> <i>C. geyseri</i>	Steele et al. 1983
<i>Pinus contorta</i> l <i>Spiraea lucida</i> P.C.	Mountains of Alberta east of Continental Divide	Cold moist	Co-climax with <i>P. mariana</i>	<i>P. mariana</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>S. lucida</i> <i>L. borealis</i> (codom) <i>C. rubescens</i>	Thompson and Kuist 1976
<i>Pinus contorta</i> l <i>Symphoricarpos albus</i> P.C.	Mountains of southwestern Alberta	Warm well- drained	Co-climax with <i>P. glauca</i> <i>P. menziesii</i> <i>A. lasiocarpa</i>	<i>P. glauca</i> <i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>S. albus</i> <i>A. cordifolia</i> <i>L. borealis</i>	Kuchar 1973
<i>Pinus contorta</i> l <i>Vaccinium caespitosum</i> C.T.	Mountains of south- central Montana, Idaho, and northern Utah	Cool well- drained	Ultimate climax unknown; probably seral or minor climax to <i>A. lasiocarpa</i> <i>P. menziesii</i>	<i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>V. caespitosum</i> <i>V. scoparium</i> <i>Festuca ovina</i> <i>L. borealis</i>	Cooper et al. 1983 ⁶ Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981
<i>Pinus contorta</i> l <i>Vaccinium globulare</i> C.T.	Mountains of southern Idaho, northwestern Wyoming, and northern Utah	Cool well- drained	Ultimate climax unknown; probably seral or minor climax to <i>A. lasiocarpa</i> <i>P. menziesii</i>	<i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>V. globulare</i> <i>L. utahensis</i> <i>V. scoparium</i> <i>C. rubescens</i>	Steele et al. 1983
<i>Pinus contorta</i> l <i>Vaccinium membranaceum</i> P.C.	Mountains of southern British Columbia	Cool moist	Co-climax with <i>P. glauca</i>	<i>P. glauca</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>V. membranaceum</i> <i>C. canadensis</i> (codom) <i>C. uniflora</i> <i>L. borealis</i>	Wali and Krajina 1973
<i>Pinus contorta</i> l <i>Vaccinium occidentale</i> P.C.	Mountains of central Oregon	Warm sea- sonally moist to wet	Seral to <i>P. contorta</i>	<i>P. contorta</i> <i>Abies magnifica</i> <i>A. concolor</i> <i>P. tremuloides</i>	<i>V. occidentale</i> <i>Spiraea menziesii</i> <i>Lonicera conjugalis</i> <i>V. caespitosum</i>	Volland 1976
<i>Pinus contorta</i> l <i>Vaccinium myrtilloides</i> P.C.	Foothills of western Alberta	Warm dry to moist	Co-climax with <i>P. glauca</i>	<i>P. glauca</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>V. myrtilloides</i> <i>Cladonia</i> spp. (codom)	Corns 1978

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus contorta</i> / <i>Vaccinium scoparium</i> C.T.; P.C.	Mountains of Montana, Idaho, northwestern Wyoming, Utah, southern Wyoming, and central Colorado; mountains of central and eastern Oregon and southeastern Washington	Cool to cold dry	Ultimate climax unknown; probably seral to <i>P. contorta</i> or <i>A. lasiocarpa</i>	<i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. albicaulis</i> <i>P. tremuloides</i> <i>P. flexilis</i> <i>A. grandis</i> <i>Tsuga heterophylla</i> <i>L. occidentalis</i> <i>P. contorta</i>	<i>V. scoparium</i> <i>C. rubescens</i> <i>A. cordifolia</i> <i>L. argenteus</i> <i>B. repens</i> <i>C. geyeri</i> <i>R. cereum</i>	Cooper et al. 1983 ^a Hall 1973 Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ^b Wirsing and Alexander 1975 Volland 1976 Youngberg and Dahms 1970
<i>Pinus contorta</i> / <i>Viburnum edule</i> P.C.	Foothills, western Alberta	Warm moist	Co-climax with <i>P. glauca</i>	<i>P. glauca</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>V. edule</i> <i>Rubus pubescens</i> (codom)	LaRoi and Hnatiuk 1980
<i>Pinus contorta</i> / <i>Xerophyllum tenax</i> C.T.	Mountains of northern Idaho	Warm moist	Ultimate climax unknown; probably seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>X. tenax</i> <i>Vaccinium</i> spp.	Cooper et al. 1983 ^a
<i>Pinus contorta</i> / <i>Calamagrostis canadensis</i> C.T.	Uinta Mountains, Utah	Cool moist	Ultimate climax unknown; probably seral or minor climax to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i>	<i>C. canadensis</i> <i>A. cordifolia</i> <i>J. communis</i> <i>Poa nervosa</i>	Mauk and Henderson 1984
<i>Pinus contorta</i> / <i>Calamagrostis rubescens</i> C.T.	Mountains of eastern Washington and Oregon, Montana, Idaho, northeastern Utah, and northwestern Wyoming	Warm dry	Ultimate climax unknown except in Blue Mts. seral to <i>A. grandis</i> Elsewhere probably seral or minor climax to <i>A. lasiocarpa</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. tremuloides</i> <i>P. contorta</i>	<i>C. rubescens</i> <i>V. scoparium</i> <i>C. geyeri</i> <i>A. cordifolia</i> <i>A. uva-ursi</i>	Hall 1973 Pfister et al. 1977 Steele et al. 1983
<i>Pinus contorta</i> / <i>Carex geyeri</i> C.T.; P.C.	Mountains of central Idaho, northwestern Wyoming, southern Wyoming, and northern and central Colorado	Cool dry	Ultimate climax unknown; probably seral to or co-climax with <i>A. lasiocarpa</i>	<i>P. contorta</i> <i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. flexilis</i> <i>P. tremuloides</i>	<i>C. geyeri</i> <i>S. oreophilus</i> <i>A. cordifolia</i> <i>L. argenteus</i> <i>B. repens</i> <i>J. communis</i>	Hess 1981 Hess and Wasser 1982 ^c Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ^b Wirsing and Alexander 1975
<i>Pinus contorta</i> / <i>Carex rossii</i> C.T.	Mountains of northwestern Wyoming	Warm dry	Ultimate climax unknown; probably seral to or co-climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. albicaulis</i>	<i>C. rossii</i> <i>L. argenteus</i> <i>P. nervosa</i>	Steele et al. 1983

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus contorta</i> / <i>Carex</i> spp.-Grass wetlands P.C.	Mountains of central Oregon	Warm seasonally wet	Seral or minor climax to <i>A. concolor</i> <i>T. mertensiana</i> except where <i>P. contorta</i> is an edaphic climax	<i>T. mertensiana</i> <i>P. tremuloides</i> <i>A. concolor</i> <i>P. contorta</i>	<i>Carex lasiocarpa</i> <i>Carex nebraskensis</i> <i>Elymus glaucus</i> <i>Arnica chamissonis</i>	Franklin and Dyrness 1973 Volland 1976
<i>Pinus contorta</i> / <i>Arnica cordifolia</i> C.T.	Mountains of eastern Idaho and northwestern Wyoming	Cool dry	Ultimate climax unknown; probably seral or minor climax to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. flexilis</i> <i>P. contorta</i>	<i>A. cordifolia</i> <i>Antennaria racemosa</i> <i>A. miser</i> <i>P. secunda</i>	Steele et al. 1983
<i>Pinus contorta</i> / <i>Lupinus argenteus</i> P.C.	Mountains of central and southern Colorado	Warm dry to well- drained	Ultimate climax unknown; probably co- climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. contorta</i>	<i>L. argenteus</i>	Steen and Dix 1974 ⁵
Populus tremuloides series and other P. tremuloides dominated vegetation						
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Berberis repens</i> C.T. <i>P. tremuloides</i> / <i>B. repens</i> C.T.	Mountains of western Wyoming	Warm to cool well- drained	Seral or minor climax to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>B. repens</i> <i>S. albus</i> <i>P. myrsinites</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> / <i>Pachistima myrsinites</i> P.C.	Mountains of central and southwestern Colorado	Warm dry	Ultimate climax unknown; probably co- climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>P. myrsinites</i> <i>V. scoparium</i> <i>C. geyeri</i>	Steen and Dix 1974 ⁵
<i>Populus tremuloides</i> / <i>Elymus glaucus</i> P.C.	Mountains of central and southwestern Colorado	Warm moist to well- drained	Ultimate climax unknown; probably co- climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>E. glaucus</i> <i>A. alnifolia</i> <i>Symphoricarpos</i> spp. <i>Liquisticum porteri</i>	Steen and Dix 1974 ⁵
<i>Populus tremuloides</i> / <i>Festuca thurberi</i> P.C.	Mountains of southwestern Colorado	Warm dry	Ultimate climax unknown; probably co- climax with <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. flexilis</i> <i>P. tremuloides</i>	<i>F. thurberi</i> <i>B. repens</i> <i>S. oreophilus</i> <i>F. ovalis</i>	Steen and Dix 1974 ⁵
<i>Populus tremuloides</i> / <i>Equisetum arvense</i> C.T.	Mountains of western Wyoming	Cool wet	Probably climax	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>E. arvense</i> <i>E. glaucus</i> <i>T. fendleri</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> / <i>Heracleum lanatum</i> C.T.	Mountains of western Wyoming	Warm moist	Seral or minor climax to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>H. lanatum</i> <i>P. bracteosa</i> <i>T. fendleri</i> <i>E. glaucus</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Pedicularis racemosa</i> C.T.	Mountains of western Wyoming	Cool moist	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i>	<i>P. racemosa</i> <i>A. cordifolia</i> <i>S. oreophilus</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> / <i>Ranunculus alismaefolius</i> C.T.	Mountains of western Wyoming	Cool moist to wet	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i>	<i>R. alismaefolius</i> <i>Carex microptera</i> <i>Trifolium longipes</i>	Youngblood and Mueggler 1981

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Rudbeckia occidentalis</i> C.T. <i>P. tremuloides</i> / <i>R. occidentalis</i> C.T.	Mountains of southeastern Idaho and western Wyoming	Cool moist to well- drained	Seral to <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. tremuloides</i>	<i>R. occidentalis</i> <i>T. longipes</i> <i>Nemophila breviflora</i> <i>Melica spectabilis</i>	Mueggler and Campbell 1982 Youngblood and Mueggler 1981
Thuja plicata series						
<i>Thuja plicata</i> / <i>Oplopanax horridum</i> H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Cool moist	Seral to <i>T. plicata</i> <i>T. heterophylla</i>	<i>T. plicata</i> <i>T. heterophylla</i> <i>L. occidentalis</i> <i>P. monticola</i> <i>A. grandis</i>	<i>O. horridum</i> <i>Athyrium</i> <i>felix-femina</i> <i>Dryopteris dilatata</i>	Cooper et al. 1983 ⁶ Daubenmire and Daubenmire 1968
<i>Thuja plicata</i> / <i>Pachistima myrsinites</i> H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Warm dry to well- drained	Seral to <i>T. plicata</i>	<i>T. plicata</i> <i>P. monticola</i> <i>L. occidentalis</i> <i>P. menziesii</i> <i>P. contorta</i> <i>A. grandis</i>	<i>P. myrsinites</i> <i>A. glabrum</i> <i>G. triflorum</i>	Daubenmire and Daubenmire 1968
<i>Thuja plicata</i> / <i>Athyrium felix-femina</i> H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Cool wet	Seral to <i>T. plicata</i>	<i>T. plicata</i> <i>P. monticola</i> <i>A. grandis</i> <i>P. menziesii</i>	<i>A. felix-femina</i> <i>G. triflorum</i> <i>S. triangularis</i> <i>S. amplexifolius</i>	Cooper et al. 1983 ⁶ Daubenmire and Daubenmire 1968
<i>Thuja plicata</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northern Idaho and northwestern Montana	Cool to warm moist	Seral to <i>T. plicata</i>	<i>T. plicata</i> <i>A. lasiocarpa</i> <i>A. grandis</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. contorta</i>	<i>A. nudicaulis</i> <i>C. uniflora</i> <i>M. ferruginea</i> <i>X. tenax</i>	Cooper et al. 1983 ⁶ Pfister et al. 1977
Pseudotsuga menziesii series						
<i>Pseudotsuga menziesii</i> / <i>Arctostaphylos uva-ursi</i> H.T.	Mountains of New Mexico	Warm dry	Minor climax to <i>P. menziesii</i> <i>P. flexilis</i>	<i>P. menziesii</i> <i>P. flexilis</i> <i>P. tremuloides</i> <i>P. engelmannii</i> <i>P. strobiformis</i> <i>A. lasiocarpa</i> <i>P. ponderosa</i>	<i>A. uva-ursi</i> <i>J. communis</i>	Fitzhugh et al. 1984 ³
<i>Pseudotsuga menziesii</i> / <i>Pachistima myrsinites</i> H.T.	Mountains of west-central Colorado	Warm dry	Minor climax to <i>P. menziesii</i>	<i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>P. myrsinites</i> <i>S. oreophilus</i> <i>A. cordifolia</i> <i>V. myrtillus</i>	Hess and Wasser 1982 ⁷
<i>Pseudotsuga menziesii</i> / Scree H.T.	Mountains of southwestern and northern New Mexico	Warm dry	Seral to <i>P. menziesii</i>	<i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. strobiformis</i>	<i>Salix</i> spp. <i>S. oreophilus</i> <i>H. dumosus</i> <i>B. ciliatus</i>	DeVelice et al. 1984 ² Fitzhugh et al. 1984 ³
Abies grandis series						
<i>Abies grandis</i> / <i>Linnaea borealis</i> H.T.	Mountains of Montana, Idaho, and eastern Washington and Oregon	Cool moist to well- drained	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>P. monticola</i> <i>P. ponderosa</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>L. borealis</i> <i>Disporum hookeri</i> <i>A. cordifolia</i> <i>V. globulare</i>	Hall 1973 Pfister et al. 1977 Steele et al. 1981
<i>Abies grandis</i> / <i>Pachistima myrsinites</i> H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Warm well- drained	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. contorta</i> <i>P. monticola</i>	<i>P. myrsinites</i> <i>G. triflorum</i> <i>S. stellata</i> <i>T. occidentale</i>	Daubenmire and Daubenmire 1968
<i>Abies grandis</i> / <i>Vaccinium caespitosum</i> H.T.	Mountains of central Idaho	Cool well- drained	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>V. caespitosum</i> <i>F. virginiana</i> <i>C. rubescens</i>	Steele et al. 1981

APPENDIX—Continued

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies grandis</i> / <i>Vaccinium globulare</i> H.T.	Mountains of central Idaho	Cool well- drained	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>V. globulare</i>	Steele et al. 1983
<i>Abies grandis</i> / <i>Vaccinium membranaceum</i> P.C.	Blue Mountains, Washington and Oregon	Warm dry	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>P. monticola</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. ponderosa</i>	<i>V. membranaceum</i> <i>A. cordifolia</i> <i>P. secunda</i>	Hall 1973
<i>Abies grandis</i> / <i>Vaccinium scoparium</i> P.C.	Blue Mountains, Washington and Oregon	Cool dry	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>P. monticola</i> <i>L. occidentalis</i>	<i>V. scoparium</i> <i>C. rubescens</i>	Hall 1973
<i>Abies grandis</i> / <i>Xerophyllum tenax</i> H.T.	Mountains of northern Idaho	Cool dry	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>P. ponderosa</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>X. tenax</i> <i>V. globulare</i>	Cooper et al. 1983 ^a
<i>Abies grandis</i> / <i>Clintonia uniflora</i> H.T.	Mountains of western Montana, and central and northern Idaho	Warm moist	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>P. contorta</i> <i>L. occidentalis</i>	<i>C. uniflora</i> <i>L. borealis</i> <i>Adenocaulon bicolor</i> <i>X. tenax</i> <i>M. ferruginea</i>	Cooper et al. 1983 ^a Pfister et al. 1977 Steele et al. 1981
<i>Abies grandis</i> / <i>Coptis occidentalis</i> H.T.	Mountains of northern Idaho	Warm moist	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. ponderosa</i> <i>P. menziesii</i>	<i>C. occidentalis</i> <i>V. globulare</i> <i>X. tenax</i> <i>S. albus</i>	Cooper et al. 1983 ^a
<i>Abies grandis</i> / <i>Senecio triangularis</i> H.T.	Mountains of northern Idaho	Warm moist	Seral to <i>A. grandis</i>	<i>A. grandis</i> <i>A. lasiocarpa</i> <i>L. occidentalis</i>	<i>S. triangularis</i> <i>A. felix-femina</i> <i>Trautvetteria</i> <i>carolinensis</i>	Cooper et al. 1983 ^a
<i>Abies concolor</i> series						
<i>Abies concolor</i> / <i>Acer glabrum</i> H.T.	Mountains of New Mexico and Arizona	Warm dry	Minor climax to <i>A. concolor</i> <i>P. menziesii</i>	<i>A. concolor</i> <i>P. menziesii</i> <i>P. pungens</i> <i>P. tremuloides</i>	<i>A. glabrum</i> <i>A. alnifolia</i> <i>B. repens</i> <i>P. myrsinites</i>	Fitzhugh et al. 1984 ³ Moir and Ludwig 1979
<i>Abies concolor</i> / <i>Vaccinium myrtillus</i> H.T.	Mountains of northern New Mexico and southern Colorado	Cool dry	Minor climax to <i>A. concolor</i> <i>P. menziesii</i>	<i>A. concolor</i> <i>P. menziesii</i> <i>P. pungens</i> <i>A. lasiocarpa</i> <i>P. tremuloides</i>	<i>V. myrtillus</i> <i>A. glabrum</i> <i>A. uva-ursi</i> <i>P. myrsinites</i> <i>R. parviflorus</i>	DeVelice et al. 1984 ²
<i>Abies concolor</i> / <i>Robinia neomexicana</i> H.T. [<i>A. concolor</i> - <i>Pseudotsuga</i> <i>menziesii</i> / <i>R. neomexicana</i> H.T.]	Mountains of New Mexico and Arizona	Warm dry	Minor climax to <i>A. concolor</i> <i>P. menziesii</i>	<i>A. concolor</i> <i>P. ponderosa</i> <i>P. menziesii</i> <i>A. lasiocarpa</i> <i>P. tremuloides</i> <i>P. strobiformis</i>	<i>S. oreophila</i> <i>R. neomexicana</i> <i>Quercus gambelii</i>	Fitzhugh et al. 1984 ³ Moir and Ludwig 1979
<i>Abies concolor</i> / <i>Alnus</i> sp.- Shrub meadow P.C.	Mountains of central Oregon	Warm moist	Minor climax to <i>A. concolor</i> <i>P. menziesii</i>	<i>A. concolor</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>P. tremuloides</i>	<i>Symphoricarpos mollis</i> <i>R. ursinus</i> <i>Alnus</i> spp. <i>Carex</i> spp.	Hopkins 1979
<i>Abies concolor</i> / <i>Erigeron eximius</i> H.T.	Mountains of northern New Mexico	Cool moist	Minor climax to <i>A. concolor</i> <i>P. menziesii</i>	<i>A. concolor</i> <i>P. menziesii</i> <i>P. pungens</i> <i>P. tremuloides</i>	<i>E. eximius</i> (<i>E. superbus</i>) <i>C. foenea</i> <i>Lathyrus</i> spp. <i>Fragaria</i> spp.	DeVelice et al. 1984 ²

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
Abies amabilis series						
<i>Abies amabilis</i> / <i>Menziesia ferruginea</i> P.C.	Mountains of southern Washington and northwestern Oregon	Cool moist	Seral to <i>A. amabilis</i>	<i>A. amabilis</i> <i>Abies procera</i> <i>P. menziesii</i> <i>T. mertensiana</i> <i>T. heterophylla</i> <i>T. plicata</i> <i>P. monticola</i>	<i>M. ferruginea</i> <i>Vaccinium</i> spp. <i>X. tenax</i> <i>C. uniflora</i> <i>S. stellata</i> <i>C. canadensis</i>	Brockway et al. 1983 Hemstrom et al. 1982
<i>Abies amabilis</i> / <i>Oplopanax horridum</i> P.C.	Mountains of northwestern Oregon	Cool wet	Seral to <i>A. amabilis</i>	<i>A. amabilis</i> <i>A. procera</i> <i>Chamaecyparis</i> <i>nootkatensis</i> <i>P. menziesii</i> <i>T. mertensiana</i> <i>T. plicata</i>	<i>O. horridum</i> <i>Vaccinium</i> spp. <i>Rubus spectabilis</i> <i>Acer circinatum</i>	Hemstrom et al. 1982
<i>Abies amabilis</i> / <i>Rhododendron albiflorum</i> P.C.	Mountains of southern Washington and northwestern Oregon	Cool wet	Seral to <i>A. amabilis</i>	<i>A. amabilis</i> <i>A. procera</i> <i>C. nootkatensis</i> <i>P. menziesii</i> <i>P. monticola</i> <i>T. mertensiana</i> <i>T. heterophylla</i> <i>T. plicata</i>	<i>R. albiflorum</i> <i>Vaccinium</i> spp. <i>C. uniflora</i> <i>M. ferruginea</i> <i>P. secunda</i> <i>Achlys triphylla</i>	Brockway et al. 1983 Hemstrom et al. 1982
<i>Abies amabilis</i> - <i>Picea engelmannii</i> / <i>Rhododendron macrophyllum</i> P.C.	Cascade Mountains, northern Oregon	Cool moist	Co-climax with <i>A. amabilis</i>	<i>A. amabilis</i>	<i>R. macrophyllum</i> <i>L. glandulosum</i> <i>C. canadensis</i>	Franklin and Dyrness 1973
<i>Abies amabilis</i> / <i>Vaccinium membranaceum</i> P.C.	Mountains of northwestern Oregon	Cool moist	Seral to <i>A. amabilis</i>	<i>A. amabilis</i> <i>A. procera</i> <i>P. menziesii</i> <i>T. mertensiana</i> <i>T. heterophylla</i>	<i>V. membranaceum</i> <i>C. uniflora</i> <i>X. tenax</i> <i>P. secunda</i>	Hemstrom et al. 1982
<i>Abies amabilis</i> / <i>Achlys triphylla</i> P.C.	Cascade Mountains, western Oregon	Cool moist	Seral to <i>A. amabilis</i> <i>T. mertensiana</i>	<i>A. amabilis</i> <i>A. grandis</i> <i>T. mertensiana</i> <i>P. monticola</i> <i>P. menziesii</i>	<i>A. triphylla</i> <i>Tiarella unifoliata</i> <i>Asarum caudatum</i>	Dyrness et al. 1974
<i>Abies amabilis</i> / <i>Tiarella unifoliata</i> P.C.	Cascade Mountains, western Oregon	Cool moist	Seral to <i>A. amabilis</i> <i>T. mertensiana</i>	<i>A. amabilis</i> <i>T. mertensiana</i> <i>P. menziesii</i> <i>A. grandis</i> lconcolor <i>P. monticola</i> <i>A. procera</i>	<i>T. unifoliata</i> <i>A. triphylla</i> <i>C. canadensis</i> <i>Vaccinium</i> spp.	Dyrness et al. 1974 Hemstrom et al. 1982
Abies magnifica series						
<i>Abies magnifica</i> / <i>Linnaea borealis</i> P.C.	Russian Peak, Klamath Mountains, California	Cool moist open	Seral to <i>A. magnifica</i>	<i>A. magnifica</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>P. contorta</i> <i>P. monticola</i> <i>T. mertensiana</i> <i>A. concolor</i> <i>Pinus lambertiana</i> <i>A. amabilis</i> <i>A. lasiocarpa</i>	<i>L. borealis</i> <i>P. secunda</i> <i>Anemone deltoidea</i> <i>C. umbellata</i>	Sawyer and Thornburgh 1977

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies magnifica</i> / <i>Leucothoe davisiae</i> P.C.	Russian Peak, Klamath Mountains, California	Cool wet	Minor climax to <i>A. magnifica</i> <i>A. amabilis</i>	<i>A. lasiocarpa</i> <i>A. concolor</i> <i>A. amabilis</i> <i>A. magnifica</i> <i>P. monticola</i> <i>Picea breweriana</i> <i>T. brevifolia</i> <i>P. lambertiana</i> <i>T. mertensiana</i> <i>Libocedrus</i> <i>decurrens</i>	<i>L. davisiae</i> <i>Ribes lacustre</i> <i>Alnus tenuifolia</i> <i>Sorbus sitchensis</i>	Sawyer and Thornburgh 1977
Tsuga heterophylla series						
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northern Idaho and northwestern Montana	Warm moist	Seral to <i>T. heterophylla</i> <i>T. plicata</i>	<i>T. heterophylla</i> <i>T. plicata</i> <i>P. monticola</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>C. uniflora</i> <i>A. nudicaulis</i>	Cooper et al. 1983 ^a Pfister et al. 1977
<i>Tsuga heterophylla</i> / <i>Gymnocarpium dryopteris</i> H.T.	Mountains of northern Idaho	Warm moist	Seral to <i>T. heterophylla</i>	<i>T. heterophylla</i> <i>A. grandis</i> <i>L. occidentalis</i> <i>T. plicata</i> <i>P. monticola</i>	<i>G. dryopteris</i> <i>P. myrsinites</i>	Cooper et al. 1983 ^a
Tsuga mertensiana series						
<i>Tsuga mertensiana</i> / <i>Menziesia ferruginea</i> H.T.	Mountains of northern Idaho, southern British Columbia, southern Washington, and central Oregon	Cool moist	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. lasiocarpa</i> <i>P. contorta</i> <i>L. occidentalis</i> <i>A. amabilis</i>	<i>M. ferruginea</i> <i>X. tenax</i> <i>R. albiflorum</i> <i>Vaccinium</i> spp.	Brockway et al. 1983 Cooper et al. 1983 ^a Daubenmire and Daubenmire 1968 Pfister et al. 1977
<i>Tsuga mertensiana</i> / <i>Phyllodoce empetriformis</i> P.C.	Russian Peak, Klamath Mountains, California	Cool moist to wet	Minor climax to <i>T. mertensiana</i>	<i>A. lasiocarpa</i> <i>P. contorta</i> <i>T. mertensiana</i> <i>P. monticola</i> <i>P. breweriana</i> <i>A. concolor</i> <i>T. brevifolia</i> <i>A. amabilis</i>	<i>P. empetriformis</i> <i>L. glandulosum</i> <i>Kalmia polifolia</i> <i>Pyrola picta</i>	Sawyer and Thornburgh 1977
<i>Tsuga mertensiana</i> / <i>Rhododendron albiflorum</i> P.C.	Mountains of southern Washington	Cool dry	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. amabilis</i> <i>T. heterophylla</i> <i>C. nootkatensis</i> <i>A. lasiocarpa</i>	<i>R. albiflorum</i> <i>M. ferruginea</i> <i>Vaccinium</i> spp. <i>P. secunda</i>	Brockway et al. 1983
<i>Tsuga mertensiana</i> / <i>Vaccinium membranaceum</i> P.C.	Mountains of southern Washington	Cool moist	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. lasiocarpa</i> <i>A. amabilis</i>	<i>V. membranaceum</i> <i>Vaccinium</i> spp.	Brockway et al. 1983
<i>Tsuga mertensiana</i> / <i>Vaccinium scoparium</i> P.C.	Mountains of northwestern Oregon	Cool dry	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. amabilis</i> <i>A. lasiocarpa</i> <i>A. procera</i> <i>P. monticola</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>V. scoparium</i> <i>V. membranaceum</i> <i>X. tenax</i> <i>C. umbellata</i>	Hemstrom et al. 1982

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Tsuga mertensiana</i> / <i>Xerophyllum tenax</i> H.T.	Mountains of northern Idaho and northwestern Montana; mountains of British Columbia, Washington, and central Oregon	Warm dry	Seral to <i>T. mertensiana</i> <i>A. lasiocarpa</i>	<i>T. mertensiana</i> <i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. monticola</i> <i>P. contorta</i> <i>P. albicaulis</i> <i>L. occidentalis</i>	<i>X. tenax</i> <i>V. membranaceum</i> <i>V. globulare</i>	Cooper et al. 1983 ^a Daubenmire and Daubenmire 1968 Pfister et al. 1977
<i>Tsuga mertensiana</i> / <i>Luzula hitchcockii</i> H.T.	Mountains of Montana west of Continental Divide, central and southern Idaho, and northwestern Wyoming	Cool well- drained	Seral to <i>T. mertensiana</i> <i>A. lasiocarpa</i>	<i>T. mertensiana</i> <i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. albicaulis</i>	<i>L. hitchcockii</i> <i>V. scoparium</i> <i>X. tenax</i> <i>A. latifolia</i>	Pfister et al. 1977
<i>Tsuga mertensiana</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northern Idaho	Warm moist	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. lasiocarpa</i> <i>P. menziesii</i> <i>P. contorta</i> <i>L. occidentalis</i> <i>P. monticola</i>	<i>C. uniflora</i> <i>X. tenax</i> <i>M. ferruginea</i>	Cooper et al. 1983 ^a
<i>Tsuga mertensiana</i> / <i>Streptopus amplexifolius</i> H.T.	Mountains of northern Idaho	Warm moist	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>A. lasiocarpa</i>	<i>S. amplexifolius</i> <i>M. ferruginea</i> <i>S. triangularis</i> <i>T. carolinensis</i>	Cooper et al. 1983 ^a
Pinus flexilis series						
<i>Pinus flexilis</i> / <i>Arctostaphylos uva-ursi</i> H.T.	Mountains of northern New Mexico and southern Colorado	Warm dry	Minor climax to <i>P. flexilis</i>	<i>P. flexilis</i> <i>P. menziesii</i> (minor climax)	<i>A. uva-ursi</i> <i>J. communis</i>	DeVelice et al. 1984 ²
<i>Pinus flexilis</i> / <i>Calamagrostis purpurascens</i> H.T.	High mountains of Colorado east of the Continental Divide	Cool dry	Minor climax to <i>P. flexilis</i>	<i>P. flexilis</i>	<i>C. purpurascens</i> <i>Carex</i> spp. <i>T. spicatum</i>	Hess 1981
<i>Pinus flexilis</i> / <i>Trifolium dasyphyllum</i> H.T.	Mountains of north-central Colorado	Cool dry	Minor climax to <i>P. flexilis</i>	<i>P. flexilis</i>	<i>T. dasyphyllum</i> <i>C. purpurascens</i> <i>C. foenea</i>	Hess 1981
<i>Pinus flexilis</i> / <i>Festuca arizonica</i> H.T.	Mountains of southern Colorado	Warm dry	Co-climax with <i>P. aristata</i>	<i>P. aristata</i> (may be pure stands on drier sites)	<i>F. arizonica</i> <i>F. thurberi</i>	DeVelice et al. 1984 ²
Pinus aristata series						
<i>Pinus aristata</i> / <i>Festuca thurberi</i> H.T.	San Juan and Sangre Cristo Mountains, Colorado	Cool dry	Co-climax with <i>P. aristata</i>	<i>P. aristata</i>	<i>F. thurberi</i> <i>R. montigenum</i> <i>Vaccinium</i> spp. <i>P. delicatum</i>	DeVelice et al. 1984 ²
<i>Pinus aristata</i> / <i>Trifolium dasyphyllum</i> H.T.	Mountains of north-central Colorado	Cool dry	Minor climax to <i>P. aristata</i>	<i>P. aristata</i>	<i>T. dasyphyllum</i> <i>C. purpurascens</i> <i>P. delicatum</i>	Hess 1981
Pinus albicaulis series						
<i>Pinus albicaulis</i> / <i>Vaccinium scoparium</i> H.T.	Mountains of northwestern Wyoming	Cool dry	Minor climax to <i>P. albicaulis</i> <i>P. contorta</i>	<i>P. albicaulis</i> <i>P. contorta</i> <i>A. lasiocarpa</i>	<i>V. scoparium</i> <i>C. rossii</i> <i>A. cordifolia</i>	Steele et al. 1983
<i>Pinus albicaulis</i> / <i>Carex rossii</i> H.T.	Mountains of northwestern Wyoming	Cool dry	Minor climax to <i>P. albicaulis</i>	<i>P. albicaulis</i> <i>A. lasiocarpa</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>C. rossii</i>	Steele et al. 1983
<i>Pinus albicaulis</i> / <i>Calamagrostis rubescens</i> P.C.	Eastside Cascades, north-central Washington	Cool dry	Seral to <i>P. albicaulis</i>	<i>P. albicaulis</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>C. rubescens</i> <i>P. myrsinites</i> <i>V. scoparium</i>	Williams and Lillybridge 1983

Habitat type, community type or plant community	Location	Site	Successional status <i>P. engelmannii</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus albicaulis</i> - <i>Abies lasiocarpa</i> H.T.	Mountains of Montana and northern Idaho	Cool dry	Seral to <i>A. lasiocarpa</i> <i>P. albicaulis</i>	<i>A. lasiocarpa</i> <i>P. albicaulis</i>	<i>V. scoparium</i> <i>A. latifolia</i> <i>Hieracium gracile</i>	Cooper et al. 1983 ^a Pfister et al. 1977
<i>Larix lyallii</i> series						
<i>Larix lyallii</i> - <i>Abies lasiocarpa</i> H.T.	High mountains of Montana west of Continental Divide, and northern Idaho	Cool dry	Seral to <i>L. lyallii</i> <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>L. lyallii</i> <i>P. contorta</i>	<i>P. empetriformis</i> <i>V. scoparium</i> <i>L. hitchcockii</i>	Cooper et al. 1983 ^a Pfister et al. 1977
<i>Larix lyallii</i> P.C.	Eastside Cascades, north-central Washington	Cool dry	Seral to <i>L. Lyallii</i>	<i>L. lyallii</i> <i>A. lasiocarpa</i> <i>P. albicaulis</i>	<i>Cassiope</i> spp. <i>V. scoparium</i> <i>P. empetriformis</i>	Williams and Lillybridge 1983
<i>Chamaecyparis nootkatensis</i> series						
<i>Chamaecyparis nootkatensis</i> / <i>Rhododendron albiflorum</i> P.C.	Cascade Mountains, southern Washington and northern Oregon	Cool wet	Seral to <i>C. nootkaten-</i> <i>sis</i>	<i>C. nootkatensis</i> <i>A. amabilis</i> <i>A. lasiocarpa</i> <i>P. menziesii</i> <i>T. mertensiana</i>	<i>R. albiflorum</i> <i>Vaccinium ovalifolium</i> <i>V. membranaceum</i>	Franklin 1966
<i>Chamaecyparis nootkatensis</i> / <i>Lysichiton americanum</i> P.C.	Mountains of southern British Columbia	Cool wet	Seral to <i>C. nootkaten-</i> <i>sis</i>	<i>C. nootkatensis</i> <i>A. amabilis</i> <i>A. lasiocarpa</i> <i>T. mertensiana</i> <i>P. menziesii</i>	<i>L. americanum</i> <i>O. horridum</i> <i>Coptis aspleniifolia</i>	Brooke et al. 1970

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⁸Komarkova, Vera. 1984. Habitat types on selected parts of the Gunnison and Uncompahgre National Forests. Preliminary report, 254 p. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Alexander, Robert R., and Wayne D. Shepperd. 1984. Silvical characteristics of Engelmann spruce. USDA Forest Service General Technical Report RM-114. 38 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

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Keywords: Silvics, silviculture, *Picea engelmannii*

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

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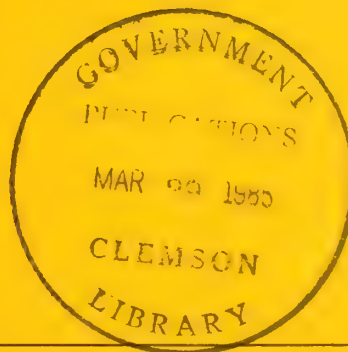
Fort Collins,
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General Technical
Report RM-115



Silvical Characteristics of Subalpine Fir

Robert R. Alexander
Raymond C. Shearer
Wayne D. Shepperd



Abstract

This report summarizes information on distribution, botanical description, habitat conditions, life history, special uses, and genetics of subalpine fir.

Silvical Characteristics of Subalpine Fir

Robert R. Alexander, Chief Silviculturist¹

Raymond C. Shearer, Principal Silviculturist²

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Contents

	Page
DISTRIBUTION	1
BOTANICAL DESCRIPTION	2
HABITAT CONDITIONS	3
Climate	3
Soils	3
Topography	4
Associated Vegetation	4
Trees	4
Understory	5
LIFE HISTORY	6
Reproduction and Early Growth	6
Flowering and Fruiting	6
Seed Production	6
Seed Dissemination	6
Seed Viability and Germinative Capacity	6
Seedling Establishment and Survival	7
Early Growth	7
Vegetative Reproduction	7
Sapling and Pole Stage to Maturity	7
Growth and Yield	7
Rooting Habit	8
Reaction to Competition	8
Silvicultural Systems and Cutting Methods	9
Damaging Agents	9
PROPERTIES AND USES OF THE WOOD	10
GENETICS	10
Population Differences	10
Races and Hybrids	10
LITERATURE CITED	10
APPENDIX. Habitat types, community types, and plant communities in which <i>Abies lasiocarpa</i> is a major climax, co-climax, minor climax, or major seral	14

Silvical Characteristics of Subalpine Fir

Robert R. Alexander, Raymond C. Shearer, and Wayne D. Shepperd

Subalpine fir, the smallest of eight species of true fir indigenous to the western United States, is distinguished by the long, narrowly conical crown terminating in a conspicuous spikelike point (fig. 1).

Two varieties are recognized: the typical variety (*Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt.) and corkbark fir (*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.). The latter, readily distinguished by its peculiar whitish, corky bark, is restricted to the Rocky Mountains of southern Colorado, Arizona, and New Mexico. Other common names for the typical variety include balsam, white balsam, alpine fir, western balsam fir, balsam fir, Rocky Mountain fir, white fir, and pino real blanco de las sierras; for corkbark fir, alamo de la sierra (Little 1979).

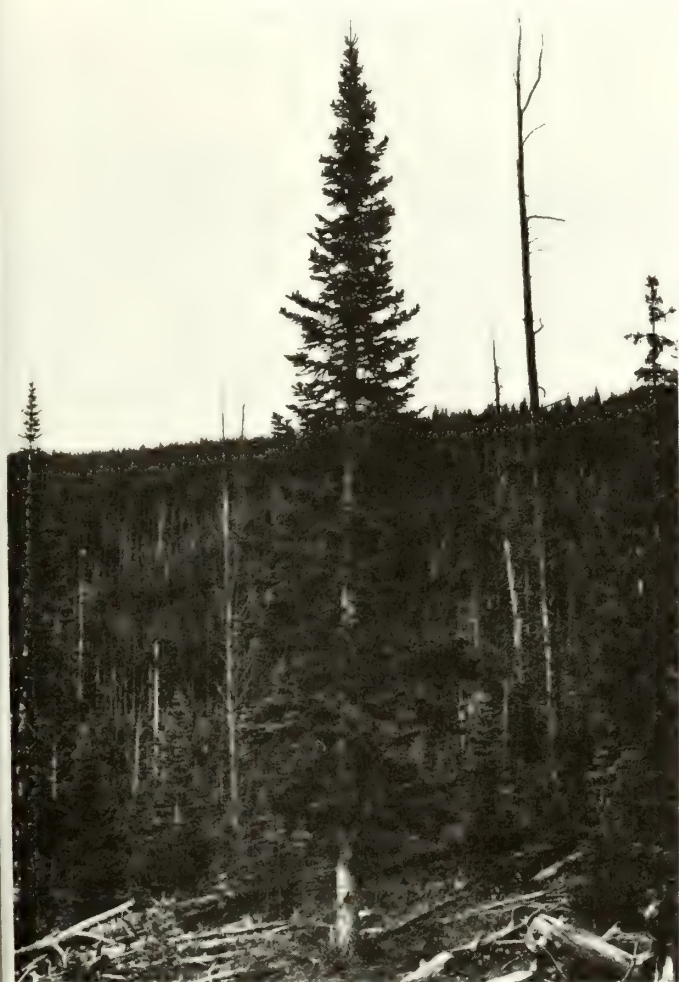


Figure 1.—Mature subalpine fir on the Fraser Experimental Forest, Colorado.

Throughout much of the Rocky Mountains, subalpine fir has no special or unique properties. By providing cover, subalpine fir assists in protecting watersheds and rehabilitating the landscape. Forests in which subalpine fir grows occupy the highest water-yielding areas in much of the west. They also provide habitat for a variety of game and nongame animals, forage for livestock, recreational opportunities, and scenic beauty. However, these properties are indigenous to the sites where subalpine fir grows rather than to any special properties associated with the species.

DISTRIBUTION

Subalpine fir is widely distributed (fig. 2). It ranges from 32° N. latitude in Arizona and New Mexico to 64°30' N. in Yukon Territory, Canada. Along the Pacific coast, the range extends from southeastern Alaska, south of the Copper River Valley (lat. 62° N.) the northwestern limit; east to central Yukon Territory (lat. 64°30' N.) the northern limit, south through British Columbia along the east slopes of the Coast Range to the Olympic Mountains of Washington, and along both slopes of the Cascades to southern Oregon. It is not found on the west slopes of the Coast Range in southern British Columbia or along the Coast Range in Washington and Oregon, but it does occur on Vancouver Island (Alexander 1958, 1965, 1980). It is also found locally in northeastern Nevada and northwestern California (Little 1971). Except where noted above, subalpine fir is a major component of high elevation Pacific Northwest forests.

In the Rocky Mountain region, subalpine fir extends from the interior valleys of British Columbia west of the Continental Divide and south of the Peace River (lat. 55° N.), south along the high elevations of the Rocky Mountain system to southern New Mexico and Arizona. In the north, its range extends from the high mountains of central British Columbia, western Alberta, northeastern Washington and northeastern Oregon, Idaho, Montana, to northwestern and north-central Wyoming. In Utah, it commonly occurs in the Uinta and Wasatch Mountains but is less abundant on the southern plateaus. The range extends from southern Wyoming, through the high mountains of Colorado and northern New Mexico, and westward through northeastern Arizona to the San Francisco Mountains (Alexander 1958, 1965, 1980). Subalpine fir is also a major component of the high-elevation forests of the Rocky Mountains.

Corkbark fir is found mixed with subalpine fir on scattered mountains in southwestern Colorado; northern, western and southwestern New Mexico; and in the high mountains of Arizona (Little 1979).

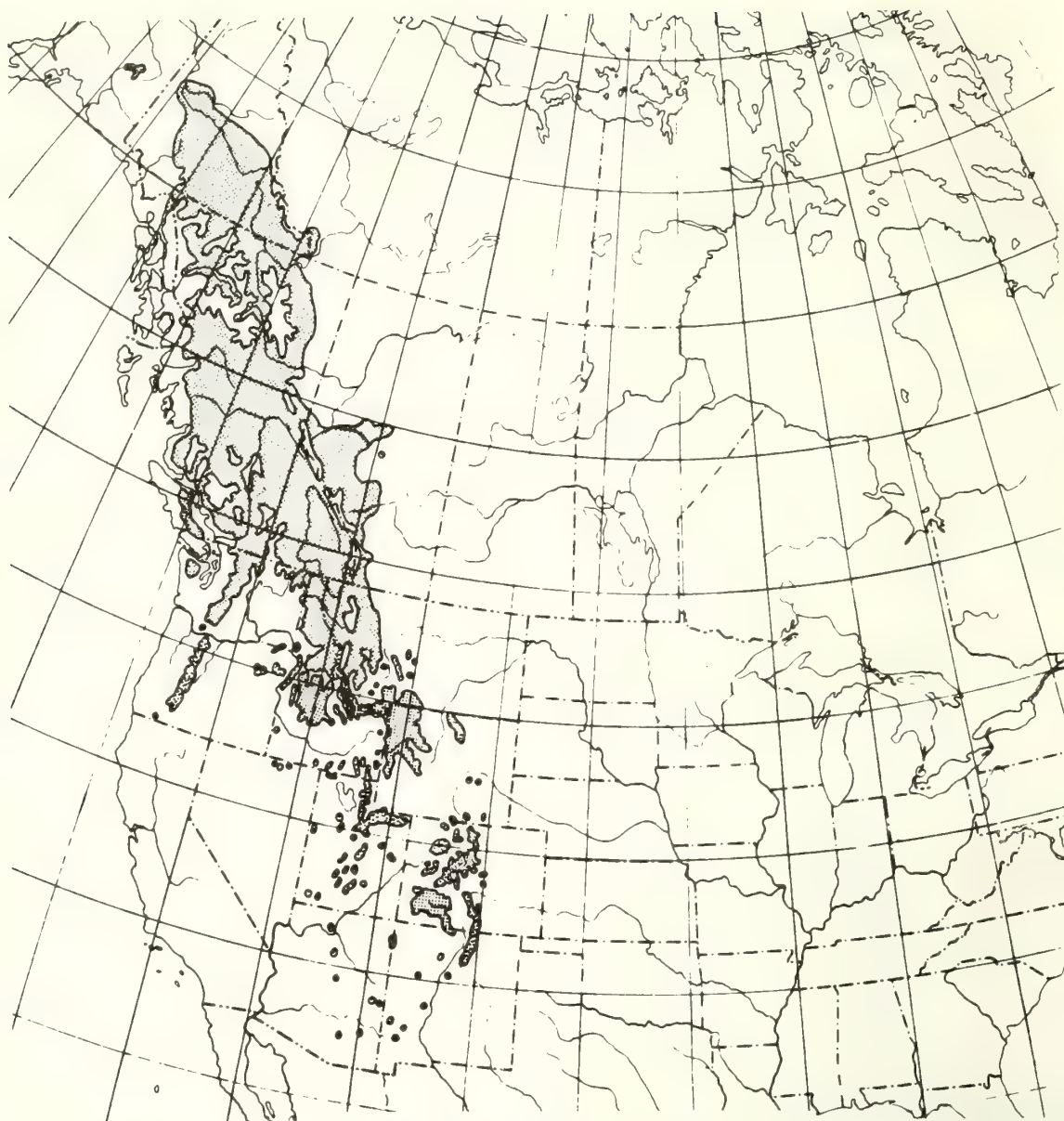


Figure 2.—Natural range of subalpine fir.

BOTANICAL DESCRIPTION

The botanical features of subalpine fir, as described by Preston (1948) and Liu (1971), are as follows:

Needles.—Needles are pale blue-green, crowded, nearly erect, and sessile. On the lower branches, they are about 1 to 1-3/4 inches long, and either flattened, blunt, or notched. On the upper branches, needles are about 1/2 inch long and pointed (fig. 3A).

Flowers.—Male flowers are usually dark indigo-blue and are borne on the lower branches (fig. 3A), while the violet-purple female flowers are borne on the upper branches.

Cones.—The cones are usually 2-1/2 to 4 inches long, ovate to cylindrical, and characteristically purplish gray to nearly black when ripe (fig. 3B). Cone scales are

longer than broad and about three times longer than the long-tipped bracts.

Seeds.—Seeds average about 1/4 inch long and have dark lustrous wings (fig. 3B).

Twigs.—The stout, pubescent twigs are pale orange, becoming smooth and gray or silver white with age.

Winter buds.—These are subglobose, resinous, and about 1/8 to 1/4 inch long, with light orange-brown scales.

Bark.—The bark is thin, gray, and smooth except for numerous resin blisters on young trees. It becomes shallowly fissured, especially near the base, with age (fig. 3C).

Wood.—Both the heartwood and sapwood, which are generally difficult to distinguish, are creamy white to pale brown, soft, stiff, fine-textured, straight-grained, and nonresinous.

HABITAT CONDITIONS

Climate

Subalpine fir grows in the coolest and wettest forested continental area of the western United States (Thornwaite 1948). Temperatures range from below -50°F in the winter to more than 90°F in the summer. Although widely distributed, subalpine fir grows within a narrow range of mean temperatures. Mean annual temperatures vary from 25°F to 40°F , with a July mean of 45°F to 60°F , and a January mean of 5°F to 25°F (Baker 1944, Haefner 1971, Marr et al. 1968) (table 1).

Average precipitation is in excess of 24 inches, much of which falls as snow. More than half of the precipitation occurs from late fall to late winter in the Pacific Northwest and west of the Continental Divide in the Rocky Mountains north of Utah and Wyoming. East of the divide in the Rocky Mountains north of New Mexico and Arizona, the heaviest precipitation comes in late winter and early spring. In the Rocky Mountains and associated ranges in Arizona and New Mexico, most precipitation comes during late summer and early fall (Baker 1944, Thornwaite 1948). However, cool summers, cold winters, and development of deep winter snowpacks are more important than total precipitation in differentiating where subalpine fir grows in relation to other species.

Soils

Information on soils where subalpine fir grows is limited. In the Pacific Coast region, soil parent materials are mixed and varied. Zonal soils in the subalpine fir zone are Cryorthods (Podzolic soils), or Haploorthods (Brown Podzolic soils) with well-developed but ultimately thin humus layers. Haploxeruts and Haplahumults (Reddish-Brown Lateritic soils) developed from volcanic lava, Xerochrepts (Regosolic soils) developed from shallow residual material, and Lithic (Lithosolic soils) are also common in some localities. Dystrandeps (Bog soils) and Haplaquepts (Humic Gley soils) occur on poorly drained situations. Soils are more acid than in lower elevation forests, with pH typically ranging from 4.5 to 5.9 (Franklin and Dyrness 1973, USDA SCS 1975).

In the Rocky Mountain subalpine zone, soil materials vary according to the character of the bedrock from which they originated. Crystalline granitic rock predominates, but conglomerates, shales, sandstones, basalts, and andesites commonly occur. Glacial deposits and stream alluvial fans are also common along valley bottoms of the great soils groups; Cryorthods (Podzolic soils) and Haploorthods (Brown Podzolic soils) occur extensively on all aspects. Aquods (Ground-water Podzolic soils) are found in the more poorly drained areas. Eutroboralfs (Grey-Wooded soils) are found where timber stands are less dense and parent material finer textured. Eutrochrepts (Brown Forest soils) occur mostly along stream terrains and sideslopes in the lower subalpine; Lithic (Lithosolic soils) occur whenever bedrock is near the surface. Dystrandeps (Bog soils)



Figure 3.—Botanical features of subalpine fir: A, needles and male flowers; B, mature cones and seeds; C, bark.

Table 1.—Climatological data for four regional subdivisions within the range of subalpine fir

Location	Average temperature			Annual precipitation	Annual snowfall	Frostfree period
	Annual	July	January			
	-----°F-----			----- inches -----		days
Pacific Northwest	30-40	45-55	15-25	24-100 +	600 +	30-60
Rocky Mountain						
Northern ¹	25-35	45-55	5-15	24-60	250 +	⁴ 30-60
Central ²	30-35	50-55	10-15	24-55	150-350 +	⁴ 30-60
Southern ³	30-40	50-60	15-20	24-40 +	200 +	⁴ 30-75

¹Includes Rocky Mountains north of Wyoming and Utah and associated ranges in eastern Washington and Oregon.

²Includes Rocky Mountains of Colorado, Wyoming and Utah.

³Includes Rocky Mountains and associated ranges of New Mexico and Arizona and plateaus of southern Utah.

⁴Least can occur any month of the year.

and Haplaquepts (Humic Gley soils) occur extensively in poorly drained upper stream valleys (Johnson and Cline 1965, USDA SCS 1975).

Regardless of the great soils groups that occur in the subalpine zone of the west, subalpine fir is not exacting in its soil requirements. It is frequently found growing on soils that are too wet or too dry for its common associates. Good growth is made on lower slopes, alluvial floodplains, and glacial moraines; and at higher elevations on well-drained fine- to medium-textured sand and silt loams, developed primarily from basalt, andesite, and shale. Growth is poor on shallow and coarse-textured soils developed from granitic and schistic rock, conglomerates, and coarse sandstones, and on saturated soils, but subalpine fir establishes on severe sites such as lava beds, tallus slopes, and avalanche tracks before any of its common associates. Under these conditions it may pioneer the site for other species or it may exclude the establishment of other species (Alexander 1958, 1965; Franklin and Mitchell 1967).

Topography

Subalpine fir grows near sea level at the northern limit of its range, and as high as 12,000 feet in the south. In the Coast Range of southeastern Alaska, it is found from sea level to 3,500 feet; in the Coast Range and interior plateaus of Yukon Territory and British Columbia, at 2,000 to 5,000 feet; and in the Olympic and Cascade Mountains of Washington and Oregon, generally at 4,000 to 6,000 feet, but as low as 2,000 feet along cold streambottoms and on lava flows and as high as 8,000 feet on sheltered slopes (Alexander 1980, Sudworth 1916).

In the Rocky Mountains of British Columbia and Alberta south of the Peace River, subalpine fir grows at 3,000 to 7,000 feet, but it is more abundant above 5,000 feet; in the Rocky Mountains of Montana and Idaho and associated ranges in eastern Washington and Oregon, at 2,000 to 11,000 feet, but it is more common at 5,000 to 9,000 feet (Kirkwood 1922, Larson 1930); in the Rocky

Mountains of Wyoming, Utah, and Colorado, usually at 9,000 to 11,000 feet, but it may be found as low as 8,000 feet and to timberline at 11,500 feet; and in the Rocky Mountains and associated ranges of New Mexico and Arizona at 8,000 to 12,000 feet, but usually on north slopes at 9,500 to 11,000 feet (Bates 1924, Marr 1961, Pearson 1931).

Associated Vegetation

Trees

In the Rocky Mountains, subalpine fir is most typically found in mixture with Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and forms the relatively stable Engelmann spruce—subalpine fir type (SAF Type 206) (Society of American Foresters 1980). It is also found in varying degrees in 16 other cover types:

SAF Type Number	Type
201	White Spruce
202	White Spruce—Paper Birch
205	Mountain Hemlock
208	Whitebark Pine
209	Bristlecone Pine
210	Interior Douglas-fir
212	Western Larch
213	Grand Fir
215	Western White Pine
216	Blue Spruce
217	Aspen
218	Lodgepole Pine
219	Limber Pine
223	Sitka Spruce
224	Western Hemlock
226	Coastal True Fir—Hemlock

Differences in elevation and latitude affects temperatures, and precipitation thereby influencing the composition of the forests where subalpine fir grows

(Daubenmire 1943).³ In Alaska and the Coast Range of British Columbia south through the Coast Range of Washington and Oregon, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr) is its common associate. In Alaska and northern British Columbia, Alaska-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) mixes with it, and where it approaches sea level, it mingles with Sitka spruce (*Picea sitchensis* (Bong.) Carr). From southern British Columbia southward through much of the Cascades, Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), mountain hemlock, and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) are the most common associates under closed forest conditions. Major timberline associates are mountain hemlock and whitebark pine (*Pinus albicaulis* Engelm.). Engelmann spruce is not a constant associate of subalpine fir except on the east slopes of the northern Cascades, and on exceptionally moist, cool habitats scattered throughout the southern and western Cascades. Engelmann spruce is a major associate of subalpine fir in the mountains of eastern Washington and Oregon. Less common associates in the Pacific Northwest include western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], noble fir (*Abies procera* Rehd.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western white pine (*Pinus monticola* Dougl. ex D. Don), western larch (*Larix occidentalis* Nutt.), and subalpine larch (*Larix lyallii* Parl.) (Alexander 1958, 1965, 1980).

From the mountains and interior plateaus of central British Columbia southward through the Rocky Mountain system, its most constant associate is Engelmann spruce. Less common associates include: in British Columbia and western Alberta, white spruce (*Picea glauca* (Moench) Voss), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.); in the Rocky Mountains of Montana and Idaho at its lower limits, western white pine, Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), western hemlock, western larch, grand fir, and western redcedar (*Thuja plicata* Donn ex D. Don); and at higher elevations, lodgepole pine, subalpine larch, mountain hemlock, and whitebark pine. In the Rocky Mountains of Wyoming, Utah, and Colorado, near its lower limits, associates are lodgepole pine, Douglas-fir, aspen, and blue spruce (*Picea pungens* Engelm.); and at higher elevations, whitebark pine, limber pine (*Pinus flexilis* James), and bristlecone pine (*Pinus aristata* Engelm.); and in the Rocky Mountains and associated ranges of New Mexico and Arizona, near its lower limits, white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), Rocky Mountain Douglas-fir, blue spruce, and aspen; and at higher elevations, corkbark fir. Subalpine fir frequently extends to timberline in the Rocky Mountains. Other species that accompany it to timberline are whitebark pine, mountain hemlock, and occasionally Engelmann spruce in the Rocky Mountains north of Utah and Wy-

oming; Engelmann spruce in the Rocky Mountains of Wyoming, Utah, and Colorado; and Engelmann spruce and corkbark fir in the Rocky Mountains and associated ranges south of Wyoming and Utah (Alexander 1958, 1965, 1980).

At timberline in the Rocky Mountains, subalpine fir and Engelmann spruce form a wind krummholz 3 to 7 feet high. On gentle slopes below timberline, subalpine fir, Engelmann spruce, and occasionally lodgepole pine grow in north-south strips 33 to 164 feet wide and several hundred yards long approximately at right angles to the direction of prevailing winds. These strips are separated by moist subalpine meadows 82 to 246 feet wide where deep snowdrifts accumulate (Billings 1969).

Understory

Understory vegetation is more variable than tree associates. In the Pacific Northwest and the Rocky Mountains and associated ranges north of Utah and Wyoming, common undergrowth species include the following: Labrador tea (*Ledum glandulosum* Nutt.), Cascades azalea (*Rhododendron albiflorum* Hook.), rusty skunkbush (*Menziesia ferruginea* Smith), woodrush (*Luzula hitchcockii* Hamet-Ahtl), Rocky Mountain maple (*Acer glabrum* Torr.), twinflower (*Linnaea borealis* L.), and heartleaf arnica (*Arnica cordifolia* Hook.) on cool, moist sites; queenscup beadleily (*Clintonia uniflora* (Schantz) Kunth), twistedstalk (*Streptopus amplexifolius* (L.) DC.), and sweetscented bedstraw (*Galium triflorum* Michx.) on warm, moist sites; dwarf blueberry (*Vaccinium caespitosum* Michx.), grouse whortleberry (*V. scoparium* Leiberger), fireweed (*Epilobium angustifolium* L.), mountain gooseberry (*Ribes montigenum* McClat.), and blue huckleberry (*V. globulare* Rydb.) on cool, dry sites; beargrass (*Xerophyllum tenax* (Pursh.) Nutt.), myrtle boxleaf (*Pachistima myrsinites* (Pursh.) Raf.), elksedge (*Carex geyeri* Boott), common juniper (*Juniperus communis* L.), white spirea (*Spiraea betulifolia* Hook.), pinegrass (*Calamagrostis rubescens* Buckl.), and big whortleberry (*V. membranaceum* (Hook.) C. L. Hitchc.) on warm, dry sites; and marshmarigold (*Caltha leptosepala* DC.), devilsclub (*Opopanax horridum* (J. E. Smith) Miq.), and bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) on wet sites (Daubenmire and Daubenmire 1968; Franklin and Dyrness 1973; Pfister 1972; Pfister et al. 1977; Steele et al. 1981, 1983).

Undergrowth characteristically found in the Rocky Mountains and associated ranges south of Idaho and Montana include the following: mountain bluebells (*Mertensia ciliata* (James) D. Don) and heartleaf bittercress (*Cardamine cordifolia* Gray) on cool, moist sites; russet buffaloberry (*Shepherdia canadensis* (L.) Nutt.), Oregon grape (*Berberis repens* Lindl.), myrtle boxleaf, elksedge, common juniper, mountain snowberry (*Symphoricarpos oreophilus* Gray), daisy fleabane (*Erigeron superbus* Rydb.), heartleaf arnica, and Arizona peavine (*Lathyrus arizonicus* Britt.) on warm, dry sites; and Rocky Mountain whortleberry (*V. myrtilloides* L.), grouse

³Classification of forest vegetation into "habitat types" based on methodology developed by Daubenmire (1952) and modified by others is available for much of the western forested lands. The known habitat types for all lands where subalpine fir grows are listed in the appendix with other descriptive material.

whortleberry, fireweed, groundsel (*Senecio sanguinoides* Rydb.), polemonium (*Polemonium pulcherrimum* Hook), prickly currant (*Ribes lacustre* (Pers.) Poir.), sidebells pyrola (*Pyrola secunda* L.), and mosses on cool, dry sites (Hess 1981; Hoffman and Alexander 1976, 1980, 1983; Moir and Ludwig 1979; Wirsing and Alexander 1975).

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting

Subalpine fir is monoecious. Male flowers (strobili), usually abundant, are borne in pendulous clusters from the axils of the needles on the sides of lower branchlets. Female flowers (strobili) are fewer and are borne erect and singly or in small groups on the uppermost branchlets of the crown. Male flowers ripen and pollen is wind-disseminated during the late spring and early summer. Cones open in mid-August to mid-October. Seed ripens from mid-September to late-October (Liu 1971, USDA Forest Service 1974).

Seed Production

Subalpine fir may begin to produce cones when they are 4 to 5 feet tall and 20 years old, but under closed-forest conditions, seed production is not significant until trees are older and taller. Corkbark fir does not begin to bear cones until about 50 years old. Maximum seed production for subalpine and corkbark fir occurs in dominant trees that are between 150 and 200 years old (USDA Forest Service 1974).

Subalpine fir is rated a good seed producer in the Pacific Northwest and in the Rocky Mountains of Idaho and Montana, with good to heavy crops borne every 3 years, and light crops or failures in between (Franklin et al. 1974, LeBaron and Jemison 1952). It is as good a seed producer as most associated true firs, but not as good as the hemlocks and Engelmann spruce. In one study covering an 11-year period at four locations in the Cascades, subalpine fir cone crops, based on the following criteria, were rated medium to very heavy in 6 years and very light to failure in the other 5 (Franklin et al. 1974).

Number of cones per tree	Crop rating
0	Failure
1-9	Very light
10-19	Light
20-49	Medium
50-99	Heavy
100+	Very heavy

In the Rocky Mountains south of Idaho and Montana, seed production of subalpine and corkbark fir has generally been considered to be poor, with more failures than good seed years. In one study in Colorado covering 42 area-seed crop years, subalpine fir was an infre-

quent seed producer. Some seed was produced in only 8 of the years, while the other 34 were complete failures (Noble and Ronco 1978). Similar results have been obtained from other seed production studies in Colorado. However, since these studies were designed to sample seed production in spruce-fir stands and since Engelmann spruce made up 90% or more of the dominant stand basal area, these results are only indicative of subalpine fir seed production in spruce-fir stands, not of individual dominant fir trees.

A number of cone and seed insects of subalpine fir have been identified but their relative importance, frequency of occurrence, and the magnitude of losses are not known (Hedlin et al. 1980, Keen 1958). Some seed is lost from cutting and storing of cones by pine squirrels (*Tamiasciurus hudsonicus fremonti* Audubon and Bachman), and after seed is shed small mammals such as deer mice (*Peromyscus maniculatus* Wagner), red-backed mice (*Clethrionomys gapperi* Vigors), mountain voles (*Microtus montanus* Peale), and western chipmunks (*Eutamias minimus* Bachman) consume a portion of the seeds (Alexander 1974). However, the quantitative losses from mammals, birds, and other causes are not known.

Seed Dissemination

Cones disintegrate when they are ripe. Scales with bracts fall away with the large, winged seeds, leaving only a central spikelike axis. Dissemination begins in September and usually is completed by the end of October in the Rocky Mountains (USDA Forest Service 1974). In the Pacific Northwest, seed dissemination begins in October and usually continues into November, but pitched-up cones may extend dissemination into December. Practically all seed is dispersed by the wind.⁴

Subalpine fir seeds are fairly large, averaging 34,800 per pound. Corkbark fir seeds are larger, averaging about 22,300 per pound. There are few data available on the seed dispersal distances. Studies designed to measure Engelmann spruce seed dispersal show similar dispersal patterns for subalpine fir. Prevailing winds influence the dispersal pattern at high elevations with about one-half of the seeds falling into openings within 100 feet of the windward timber edge. Seedfall continues to diminish until about two-thirds of the way across the opening and then levels off before slightly increasing about 50 feet from the leeward timber edge (Noble and Ronco 1978). Thermal upslope winds are important in seed dispersal in mountainous terrain at mid to lower elevations (Shearer 1980).

Seed Viability and Germinative Capacity

Subalpine fir seed viability is only fair; average germinative capacity is 34% and vitality transient (USDA Forest Service 1974). However, observations and limited

⁴Personal communication with Dr. J. F. Franklin, Chief Plant Ecologist, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oreg.

studies in the Rocky Mountains indicate that germinative capacity is often less than 30% (Shearer and Tackle 1960). Some lots of stored seeds exhibit embryo dormancy, which can be broken by stratification in moist sand or peat at 41° F for 60 days (USDA Forest Service 1974).

Seedling Establishment and Survival

Under natural conditions, fir seeds lie dormant under the snow and germinate the following spring. Although germination and early survival of subalpine fir is generally best on exposed mineral soil and moist humus, it is less exacting in its seedbed requirements than most of its common associates. Subalpine fir has been observed to germinate and survive on a wide variety of other seedbed types including the undisturbed forest floor, undecomposed duff and litter, and decaying wood (Alexander 1958, 1965; Clark 1969; Day 1964). Subalpine fir also invades and establishes on severe sites such as recent burns, lava flows, talus slopes, avalanche tracks, and climatically severe regions near timberline (Franklin and Mitchell 1967). Success of subalpine fir on these open sites results from its ability to establish a root system under conditions too severe for its less hardy associates, and its ability to reproduce by layering.

Although subalpine fir grows under nearly all light intensities found in nature, establishment and early survival are usually favored by shade. In the absence of Pacific silver fir, grand fir, and mountain hemlock, subalpine fir will survive under closed forest conditions with less light than Engelmann spruce, noble fir, and white spruce (Franklin and Mitchell 1967). When grown with Pacific silver and grand fir, and/or mountain hemlock, subalpine fir does not compete successfully under closed forest conditions. It cannot compete successfully with the spruces, lodgepole pine, or Rocky Mountain Douglas-fir when light intensity exceeds 50% of full shade (Alexander 1958, 1965).

Subalpine fir is restricted to cold, humid habitats because of low tolerance to high temperatures. Newly germinated subalpine fir seedlings tolerate high solar radiation but they are susceptible to heat girdling and drought. Seedlings are also killed or damaged by spring frosts, competing vegetation, frost heaving, damping off, snowmold, birds, rodents, and trampling and browsing by large animals, but losses are no different than for any common associate (Alexander 1974).

The number of seeds required to produce a first-year seedling, and an established seedling (at least 3 years old), and the number of first-year seedlings that produce an established seedling vary considerably, depending upon seed production, distance from source, seedbed, and other environmental conditions. In one study in Colorado, covering the period 1961 to 1975 and a wide variety of conditions, an average of 150 seeds (range 35-290) was required to produce a first-year seedling, and an average of 755 seeds (range 483-1,016) to produce an established seedling. For every established seedling, it required an average of 10 first-year seed-

lings, with a range of as few as 4 to as many as 14 (Noble and Ronco 1978).

Early Growth

Early growth of subalpine fir is very slow. The root length of first-year seedlings in one study in British Columbia averaged only 2.7 inches (Eis 1965). No comparable data are available in the United States, but first-year penetration of corkbark fir in Arizona averaged 3.4 inches (Jones 1971).

Shoot growth is equally slow at high elevations. First-year seedlings are frequently less than 1 inch tall. Mean annual height growth of seedlings during the first 10-20 years is usually not much better (fig. 4). In one study, seedlings 15 years old averaged only 11 inches in height on burned-over slopes, 10 inches on cutover, dry slopes, and 6 inches on cutover, wet flats (Hodson and Foster 1910). In another study, seedlings grown on mineral soil averaged only 24 inches in height after 21 years (Herring and McMin 1980). In general, trees reach 4 to 5 feet in height in about 20 to 40 years under favorable environmental and stand conditions. However, trees less than 5 inches in diameter are often 100 or more years old at higher elevations, and trees 4 to 6 feet high and 35 to 50 years old are common under closed-forest conditions (fig. 5) (Kirkwood 1922, Oosting and Reed 1952).

At lower elevations, seedling shoot growth is somewhat better. In one study in the intermountain west, average annual height growth of subalpine-fir seedlings for the first 10-years after release was 4.5 inches on clearcuts and 3.2 inches on partial cuts (McCaughy and Schmidt 1982).

Vegetative Reproduction

Subalpine fir frequently reproduces by layering where the species is a pioneer in developing forest cover on severe sites such as lava flows and talus slopes or near timberline (Franklin and Mitchell 1967). Under closed forest conditions, reproduction by layering is of minor importance.

Sapling and Pole Stage to Maturity

Growth and Yield

Natural Stands.—On exposed sites near timberline, subalpine fir is often reduced to a prostrate shrub, but under closed forest conditions, it attains diameters of 12 to 24 inches and heights of 45 to 100 feet, depending upon site quality and stand density (fig. 6). Trees larger than 30 inches in diameter and 130 feet tall are exceptional (Harlow and Harrar 1937, Sudworth 1916).

Growth is not rapid; trees 10 to 20 inches in diameter are often 150 to 200 years old under closed forest conditions. Trees older than 250 years are not uncommon. But because the species suffers severely from heartrot, many trees either die or are complete culls at an early age.

Few data are available on the yields of subalpine fir in natural stands. It usually grows in mixed stands and comprises only a minor part of the volume. In the Rocky Mountains and Pacific Northwest where it grows in association with Engelmann spruce, subalpine fir usually makes up only 10-20% of the sawlog volumes, which may vary from less than 5,000 to 40,000 fbm or more per acre (Hodson and Foster 1910, Miller and Choate 1964).

In the Pacific Northwest and Rocky Mountains, where subalpine fir grows with other true firs and/or mountain hemlock, few trees reach minimum merchantable size before being crowded out of the stand (Franklin and Mitchell 1967). Subalpine fir in the Rocky Mountains grows in pure stands most often on sites so severe that it has little commercial value. In the Pacific Northwest, pure stands on commercial sites typically occur on south slopes and are usually less than 150 years old. These stands are not extensive but are quite distinctive.⁴

Managed Stands.—The only data available for yields of subalpine fir in managed stands are estimates from simulations for mixed Engelmann spruce—subalpine fir stands in the Rocky Mountains south of Idaho and Montana (Alexander and Edminster 1980, Edminster 1978).



Figure 4.—Subalpine fir seedlings average less than 15 inches tall after 15 years in the open.



Figure 5.—Subalpine fir advanced reproduction released by removal of the overstory. Trees average 3 to 6 feet tall and area at least 50 years old.

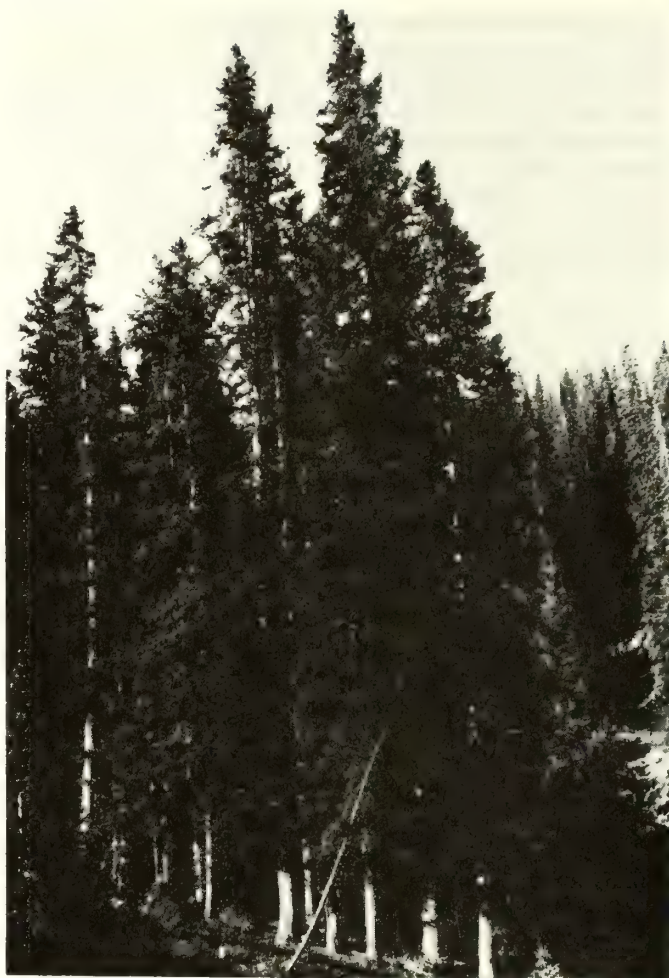


Figure 6.—Dominant subalpine firs on the Fraser Experimental Forest, Colorado. These trees are about 12 to 14 inches in diameter, about 60 feet tall, and over 200 years old at d.b.h.

These simulations show that periodic thinning to control stand density and maintain growth rates increases the yield and size of individual fir trees in these mixed stands. Furthermore, the growth rates for fir are comparable to those for spruce. However, the fir component will be substantially reduced over time by repeat thinning, so that the stand at the time of final harvest will be almost pure Engelmann spruce.

Rooting Habit

Subalpine fir has a shallow root system where it grows in situations that limit the depth of root penetration, and the superficial lateral root system common to the seedling stage persists to old age. Under more favorable conditions, subalpine fir develops a relatively deep lateral root system.

Reaction to Competition

In the Rocky Mountains and Pacific Northwest where subalpine fir and Engelmann spruce form the spruce-fir type, and mountain hemlock and other true firs are ab-

sent or limited in number, subalpine fir is very shade-tolerant (Franklin and Mitchell 1967). It is considerably more tolerant than spruce and other common associates such as lodgepole pine, quaking aspen, blue spruce, and Rocky Mountain Douglas-fir (Baker 1949). In most of the Cascades and in the Rocky Mountains where subalpine fir grows with the more shade-tolerant Pacific silver fir, grand fir, and mountain hemlock, some ecologists classify it as intolerant relative to these associates (Franklin and Mitchell 1967).

Subalpine fir together with Engelmann spruce forms a climax or long-lived seral forest vegetation throughout much of its range. In the Rocky Mountains of British Columbia and Alberta, and south of Montana and Idaho, subalpine fir and Engelmann spruce occur as either codominants or in pure stands of one or the other. Spruce, however, is most likely to form pure stands, especially at upper elevations. In the Rocky Mountains of Montana and Idaho, and the mountains of eastern Oregon and Washington, subalpine fir is a major climax. Engelmann spruce may be either a major climax or a persistent long-lived seral. Pure stands of either species may occur, but subalpine fir is most likely to form pure stands, especially at higher elevations (Alexander 1980).

Although subalpine fir is a dominant element in a number of climax or near-climax vegetation associations, these forests differ from most climax forests in that most stands are not truly all-aged. For example, in spruce-fir forests, some stands are single-storied while others are two-, three-, and multi-storied. Multi-storied stands may result from past disturbances such as fire, insect epidemics, or cutting, or they may result from the gradual deterioration of single- and two-storied stands associated with normal mortality from wind, insects, and diseases (Alexander 1974). On the other hand, some multi-storied stands appear to have originated as uneven-aged stands and are successfully perpetuating that structure (Hanley et al. 1975).

Where subalpine fir is a component of the climax vegetation, the natural tendency is for subalpine fir to reestablish itself when destroyed and temporarily replaced by other vegetation. Throughout most of the Cascades and in the Rocky Mountains where subalpine fir grows with the other true firs and/or mountain hemlock, it is seral (Franklin and Mitchell 1967).

The ecophysiology of subalpine fir in relation to common associated species is becoming better understood. Kaufmann (1982a, 1982b, 1984a, 1984b), Kaufmann and Troendle (1981), and Kaufmann et al. (1982), summarized what is known about the general water relations of subalpine fir as follows: (1) needle water vapor conductance (directly proportional to stomatal opening) is controlled primarily by visible irradiance and absolute humidity difference from needle to air (evaporative demand) with secondary effects from temperature and water stress; (2) nighttime minimum temperatures below 39° F retard stomatal opening the next day; (3) stomata function well from early spring to late fall, and high transpiration rates occur even with considerable snow-pack on the ground; (4) leaf water vapor conductance is lower than that of Engelmann spruce, lodgepole pine,

and aspen, the common associates of central Rocky Mountain subalpine forests; (5) subalpine fir trees have a larger total needle area per unit of sapwood water-conducting tissue than the other three species; and (6) subalpine fir trees have a slightly lower needle area per unit of bole or stand basal area than Engelmann spruce, but greater than lodgepole pine or aspen. At equal basal area, annual canopy transpiration of subalpine fir is about 35% lower than spruce, but 15% higher than lodgepole pine, and 110% higher than aspen. These high rates of transpiration cause subalpine fir to occur primarily on the wetter sites, generally in association with Engelmann spruce.

Silvicultural Systems and Cutting Methods

Both even- and uneven-aged silvicultural systems can be used in stands where subalpine fir is a component (Alexander 1974, 1977; Alexander and Engelby 1983; Shearer 1980). The appropriate even-aged cutting methods are clearcutting and shelterwood cutting and their modifications. The seed-tree method cannot be used because of the susceptibility of subalpine fir to windthrow. The uneven-aged cutting methods are individual-tree and group selection and their modifications. In spruce-fir stands, shelterwood and individual-tree selection methods will favor subalpine fir over Engelmann spruce, lodgepole pine, and Douglas-fir. In stands where subalpine fir grows with Pacific silver fir, grand fir, and/or mountain hemlock, clearcutting and group selection cutting will favor subalpine fir (Franklin and Mitchell 1967).

Damaging Agents

Windfall.—Subalpine fir is susceptible to windthrow. While this tendency is generally attributed to a shallow root system, root rots, soil depth, drainage, and stand conditions influence the development of the root system. The kind and intensity of cutting and topographic exposure to wind also influence the likelihood of trees being windthrown (Alexander 1974).

Insects.—Subalpine fir is attacked by several insects. In spruce-fir forests, the most destructive insect pests are the western spruce budworm (*Choristoneura occidentalis* Freeman) and western balsam bark beetle (*Dryocoetes confusus* SW). The fir engraver (*Scolytus ventralis* LeConte) may at times be very destructive locally (Furniss and Carolin 1977). In the Cascades, the balsam woolly aphid (*Adelges piceae* Ratzeburg), introduced from Europe, is the most destructive insect pest. This insect has caused significant mortality to subalpine fir, virtually eliminating it from some stands in Oregon and southern Washington (Franklin and Mitchell 1967).

Diseases.—Fir broom rust (*Melampsorella caryophyllacearum* Schroet.) and wood-rotting fungi are responsible for most disease losses (Bier et al. 1948, Hinds et al. 1960, Peterson 1963). Important root and butt rots are *Gloeocystidiellum radiosum* (Fr.) Boid., *Coniophora pu-*

teana (Schum. Fr.) Karst., *Armillaria mellea* (Vahl. ex Fr.) Quel., *Coniophorella olivacea* (Fr.) Karst., *Polyporus tomentosus* var. *circinatus* (Fr.) Satory et. Marre, and *Pholiota squarrosa* (Fr.) Kumm. Important trunk rots are *Haematostereum sanguinolentum* (Arb. ex Schw. ex Fr.) Pouz., *Phellinus pini* (Tore ex Fr.) Pilat, and *Amylostereum chailletii* (Pers. ex Fr.) Boid. Wood rots and broom rust weaken affected trees and predispose them to windthrow and windbreak.

Fire.—Subalpine fir bark is thin, especially on younger trees; lower limbs persist after death. These characteristics make subalpine fir susceptible to death or severe injury from fire.

PROPERTIES AND USES OF THE WOOD

Subalpine fir wood is light in weight, low in bending and compressive strength, moderately limber, soft, and low in resistance to shock. Shrinkage of wood is rated low to moderately high. It is easy to work, glues well, and holds nails and screws fairly well (USDA Forest Service 1955).

Fir is used as lumber in building construction, boxes, crates, planing mill products, sashes, doors, frames, and food containers. It has not been widely used for pulpwood because of inaccessibility, but it can be pulped readily by the sulfate, sulfite, or groundwood processes (USDA Forest Service 1955).

GENETICS

Population Differences

Information on subalpine fir population differences is virtually nonexistent. Undoubtedly any species with the range in elevation and latitude of subalpine fir will exhibit ecotypic variations in growth, phenology, dormancy, resistance to heat and cold, etc., among different populations.

Races and Hybrids

Corkbark fir is the only recognized natural geographical variety of subalpine fir (Little 1979). Like many species with wide distribution, unknown races and hybrids have probably developed, and there is some evidence that natural introgressive hybridization between subalpine fir and balsam fir occurs where they grow together in Canada. Horticultural and ornamental cultures have been recognized (Liu 1971). These include: (1) *Abies lasiocarpa* cv. *beissneri*, a dwarf tree bearing distorted branches and twisted needles; (2) *Abies lasiocarpa* cv. *coerulescens*, a beautiful tree with specially intensive bluish needles; (3) *Abies lasiocarpa* cv. *compacta*, a dwarf tree of compact habit.

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APPENDIX

Habitat types, community types, and plant communities in which *Abies lasiocarpa* is a major climax, co-climax, minor climax, or major seral

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> series						
<i>Abies lasiocarpa</i> / <i>Acer glabrum</i> H.T.	Mountains of central and southern Idaho, northern and central Utah, and northwestern Wyoming; mountains of northern New Mexico	Warm moist	Climax	<i>Picea engelmannii</i> <i>Pseudotsuga menziesii</i> <i>Pinus contorta</i> <i>Populus tremuloides</i> <i>Abies concolor</i> <i>Picea pungens</i>	<i>A. glabrum</i> <i>Thalictrum occidentale</i> <i>Thalictrum fendleri</i> <i>Osmorhiza chilensis</i> <i>Arnica cordifolia</i> <i>Berberis repens</i>	Alexander et al. 1984b ¹ Mauk and Henderson 1984 Steele et al. 1981 Steele et al. 1983 Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Alnus sinuata</i> H.T.	Mountains of northern Montana and central Idaho	Cool moist	Climax	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>Larix occidentalis</i>	<i>A. sinuata</i> <i>Xerophyllum tenax</i> <i>Vaccinium scoparium</i> <i>Vaccinium globulare</i>	Pfister et al. 1977 Steele et al. 1981
<i>Abies lasiocarpa</i> / <i>Berberis repens</i> H.T.	Mountains of Utah, northwest- tern Wyoming, and southeastern Idaho	Warm-cool well-drained	Climax	<i>P. engelmannii</i> (minor climax) <i>P. contorta</i> <i>P. pungens</i> <i>P. menziesii</i> <i>Pinus flexilis</i> <i>A. concolor</i> <i>P. tremuloides</i>	<i>B. repens</i> <i>Ribes montigenum</i> <i>Carex geyeri</i> <i>Pachistima myrsinites</i> <i>Symphoricarpos</i> <i>oreophilus</i>	Mauk and Henderson 1984 Pfister 1972 Steele et al. 1983 Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Clematis pseudoalpina</i> H.T.	Mountains of Montana, east of Continental Divide	Warm dry	Climax	<i>P. engelmannii</i> <i>P. flexilis</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>C. pseudoalpina</i> <i>Clematis tenuiloba</i>	Pfister et al. 1977
<i>Abies lasiocarpa</i> / <i>Juniperus communis</i> H.T.	Mountains of central Idaho, northwestern Wyoming, Utah, northern Arizona, and New Mexico	Warm to cold dry	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>A. concolor</i> (NM,AZ) <i>P. pungens</i> (UT) <i>Pinus longaeva</i> (UT)	<i>J. communis</i> <i>Pyrola secunda</i> <i>Shepherdia canadensis</i> <i>A. cordifolia</i> <i>S. oreophilus</i> <i>Rosa woodsii</i>	Mauk and Henderson 1984 Moir and Ludwig 1979 Steele et al. 1981 Steele et al. 1983 Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Linnaea borealis</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> (L. <i>borealis</i> P.C.(CO)	Mountains of north central Washington, Montana, central and southern Idaho, northwestern Wyoming, and central Colorado	Cool moist to well- drained	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>A. concolor</i>	<i>L. borealis</i> <i>V. scoparium</i> <i>Calamagrostis</i> <i>rubescens</i> <i>A. cordifolia</i>	Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ³ Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Menziesia ferruginea</i> H.T.	Mountains of southeastern Washington, eastern Oregon, Montana, Idaho, and northwestern Wyoming	Cool moist	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>Pinus monticola</i>	<i>M. ferruginea</i> <i>Rhododendron</i> <i>albiflorum</i> <i>Ledum glandulosum</i> <i>V. globulare</i> <i>Arnica latifolia</i> <i>X. tenax</i>	Cooper et al. 1983 ⁴ Daubenmire and Daubenmire 1968 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Oplopanax horridum</i> H.T.	Mountains of northern Montana	Cool moist- wet	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. monticola</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>O. horridum</i> <i>Taxus brevifolia</i>	Pfister et al. 1977
<i>Abies lasiocarpa</i> / <i>Pachistima myrsinites</i> H.T.	Mountains of southern British Columbia and north-central Washington; Rocky Mountains and associated ranges of Canada, south to southern Colorado	Warm dry to well- drained	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. monticola</i> <i>L. occidentalis</i> <i>P. tremuloides</i>	<i>P. myrsinites</i> <i>Clintonia uniflora</i> <i>Galium triflorum</i> <i>C. geyeri</i> <i>Erigeron</i> spp.	Daubenmire and Daubenmire 1968 Hess and Wasser 1982 ⁵ McLean 1970 Steen and Dix 1974 ³ Williams and Lillybridge 1983
<i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>P. myrsinites</i> H.T.						
<i>Abies lasiocarpa</i> / <i>Physocarpus malvaceus</i> H.T.	Mountains of eastern Idaho, northwestern Wyoming, and northern and central Utah	Warm moist	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>P. malvaceus</i> <i>Symphoricarpos albus</i> <i>Spiraea betulifolia</i> <i>Amelanchier alnifolia</i> <i>Sorbus scopulina</i>	Mauk and Henderson 1984 Steele et al. 1983 Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Phyllodoce</i> <i>emptriformis</i> P.C.	Eastside Cascades, north-central Washington	Cool moist	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>Pinus albicaulis</i>	<i>P. emptriformis</i> <i>V. scoparium</i>	Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Ribes montigenum</i> H.T.	Mountains of southern Montana, Idaho, Utah, and northwestern Wyoming	Cool dry	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>R. montigenum</i> <i>A. latifolia</i> <i>T. fendleri</i> <i>Antennaria microphylla</i> <i>Mertensia arizonica</i>	Mauk and Henderson 1984 Pfister 1972 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Rhododendron</i> <i>albiflorum</i> P.C.	Eastside Cascades, north-central Washington	Cool moist	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>R. albiflorum</i> <i>L. glandulosum</i>	Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Rubus parviflorus</i> H.T.	Mimbres and Mogollon Mountains, New Mexico; San Juan Mountains, Colorado	Cool moist	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> (NM) <i>A. concolor</i> (NM) <i>P. tremuloides</i>	<i>R. parviflorus</i> <i>Vaccinium myrtillus</i> <i>A. glabrum</i> <i>P. myrsinites</i>	DeVelice et al. 1984 ⁶ Fitzhugh et al. 1984 ⁷ Moir and Ludwig 1979
<i>Abies lasiocarpa</i> / <i>Salix glauca</i> H.T.	High mountains of Colorado	Cold wet	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. flexilis</i>	<i>S. glauca</i> <i>V. myrtillus</i> <i>Polemonium</i> <i>pulcherrimum</i> <i>Acomastylis rossii</i>	Hess 1981 Hess and Wasser 1982 ⁵ Komarkova 1984 ⁸
<i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>S. glauca</i> H.T.						
<i>Abies lasiocarpa</i> / <i>Shepherdia canadensis</i> H.T. (WY)	Bighorn Mountains, Wyoming; high mountains of central Colorado	Cool-warm dry	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. menziesii</i>	<i>S. canadensis</i> <i>V. scoparium</i>	Hoffman and Alexander 1976 Steen and Dix 1974 ³
<i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>S. canadensis</i> P.C.(CO)						
<i>Abies lasiocarpa</i> / <i>Spiraea betulifolia</i> H.T.	Mountains of central and southern Idaho and northwestern Wyoming	Warm dry	Climax	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. albicaulis</i>	<i>S. betulifolia</i> <i>P. myrsinites</i> <i>C. rubescens</i>	Steele et al. 1981 Steele et al. 1983

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Symphoricarpos albus</i> H.T.	Mountains of southeast Idaho and northwestern Wyoming	Warm well- drained	Climax	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>S. albus</i> <i>A. alnifolia</i> <i>C. rubescens</i>	Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Vaccinium caespitosum</i> H.T.	Mountains of Montana, central Idaho, and northern and central Utah	Cool well- drained	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>V. caespitosum</i> <i>L. borealis</i> <i>C. rubescens</i> <i>V. scoparium</i> <i>A. cordifolia</i>	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Vaccinium globulare</i> H.T.	Mountains of south-central Montana, central and southern Idaho, north- ern, Utah, and northwestern Wyoming	Cool well- drained	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>V. globulare</i> <i>V. scoparium</i> <i>Lonicera utahensis</i> <i>P. myrsinites</i>	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Vaccinium</i> <i>membranaceum</i> H.T.(UT); P.C.(OR,WA)	Blue Mountains; Washington and Oregon; mountains of central Utah	Warm dry to well- drained	Climax	<i>P. engelmannii</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>V. membranaceum</i> <i>P. myrsinites</i> <i>A. cordifolia</i> <i>Carex rossii</i>	Hall 1973 Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Vaccinium myrtillus</i> H.T.	Mogollon Plateau, Arizona; mountains of northern New Mexico and southern Colorado;	Cool moist to well- drained	Climax (AZ) co-climax with <i>P. engelmannii</i> (NM,CO,UT)	<i>P. engelmannii</i> <i>Pinus aristata</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>A. concolor</i> <i>P. flexilis</i>	<i>V. myrtillus</i> <i>Disporum</i> <i>trachycarpum</i> <i>Calamagrotis</i> <i>canadensis</i> <i>Polemonium flavum</i> <i>V. scoparium</i> <i>L. borealis</i> <i>R. parviflorus</i>	Alexander et al. 1984b ¹ DeVilce et al. 1984 ⁶ Fitzhugh et al. 1984 ⁷ Moir and Ludwig 1979 Youngblood 1984 ²
[<i>A. lasiocarpa</i> / <i>V. myrtillus</i> <i>Linnaea borealis</i> H.T.] [<i>A. lasiocarpa</i> / <i>V. myrtillus</i> - <i>Rubus parviflorus</i> H.T.] [<i>A. lasiocarpa</i> / <i>Vaccinium</i> <i>scoparium</i> - <i>L. borealis</i> H.T.]	La Sal Mountains, Utah					
<i>Abies lasiocarpa</i> / <i>Vaccinium scoparium</i> H.T.	Mountains of British Columbia and Alberta south to Arizona and New Mexico; mountains of eastern Oregon and eastern and north-central Washington	Cool dry	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>L. occidentalis</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. pungens</i> <i>A. concolor</i>	<i>V. scoparium</i> <i>C. rubescens</i> <i>V. myrtillus</i> <i>A. cordifolia</i> <i>C. geyeri</i> <i>Erigeron superbus</i> (<i>E. eximius</i>) <i>L. borealis</i> <i>P. myrsinites</i> <i>P. empetriformis</i>	Daubenmire and Daubenmire 1968 Hall 1973 Hess 1981 Hess and Wasser 1982 ⁵ Hoffman and Alexander 1976 Hoffman and Alexander 1980 Hoffman and Alexander 1983 Komarkova 1984 ⁸ Mauk and Henderson 1984 McLean 1970 Pfister 1972 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ³ Williams and Lillybridge 1983 Wirsing and Alexander 1975
<i>A. lasiocarpa</i> - <i>Pinus albicaulis</i> / <i>Vaccinium scoparium</i> H.T.	Mountains of Montana east of Continental Divide	Cool dry	Co-climax with <i>P. albicaulis</i>	<i>P. albicaulis</i> <i>P. engelmannii</i> <i>P. contorta</i>	<i>V. scoparium</i> <i>X. tenax</i> <i>C. geyeri</i> <i>A. latifolia</i>	Pfister et al. 1977

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Vaccinium</i> spp. P.C.	Eastside Cascades, north-central Washington	Cool dry	Co-climax with <i>P. engelmannii</i> <i>P. menziesii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>L. occidentalis</i>	<i>Vaccinium</i> spp. <i>C. rossii</i> <i>P. myrsinites</i> <i>Arctostaphylos uva-ursi</i>	Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Xerophyllum tenax</i> H.T.	Mountains of northern Idaho and eastern Washington and Oregon, south to southern Idaho, Montana, and north- western Wyoming	Warm dry	Climax	<i>P. engelmannii</i> <i>P. albicaulis</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>X. tenax</i> <i>V. membranaceum</i> <i>V. scoparium</i> <i>V. globulare</i> <i>Luzula hitchcockii</i>	Cooper et al. 1983 ⁴ Daubenmire and Daubenmire 1968 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Calamagrostis</i> <i>canadensis</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>C. canadensis</i> H.T. [<i>P. engelmannii</i> / <i>C. canadensis</i> H.T.]	Mountains of central Montana, Idaho, northwestern Wyoming, northern Utah, and north- central and western Colorado	Cool wet	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. menziesii</i>	<i>C. canadensis</i> <i>G. triflorum</i> <i>V. caespitosum</i> <i>L. glandulosum</i> <i>Senecio triangularis</i>	Cooper et al. 1983 ⁴ Hess 1981 Komarkova 1984 ⁴ Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Calamagrostis</i> <i>ruibescens</i> H.T.	Mountains of north- central Washington, Montana east of Continental Divide, central and southern Idaho, northern Utah, and northwestern Wyoming	Warm dry	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>C. rubescens</i> <i>O. chilensis</i> <i>T. occidentale</i> <i>C. geyseri</i> <i>A. cordifolia</i> <i>P. myrsinites</i>	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Williams and Lillybridge 1983
<i>Abies lasiocarpa</i> / <i>Luzula hitchcockii</i> H.T.	Mountains of Montana west of Continental Divide, Idaho, and north- western Wyoming	Cool well- drained	Climax	<i>P. engelmannii</i> <i>P. albicaulis</i> <i>P. contorta</i>	<i>L. hitchcockii</i> <i>A. latifolia</i> <i>X. tenax</i> <i>A. cordifolia</i> <i>M. ferruginea</i> <i>V. scoparium</i>	Cooper et al. 1983 ⁴ Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Carex geyseri</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>C. geyseri</i> H.T. [<i>P. engelmannii</i> / <i>C. geyseri</i> H.T.]	Mountains of central Montana, central Idaho, southern Utah, northwestern Wyoming southern Wyoming, and north- central and western Colorado	Warm to cool, dry	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. tremuloides</i>	<i>C. geyseri</i> <i>S. oreophilus</i> <i>A. cordifolia</i> <i>Lupinus argenteus</i> <i>B. repens</i> <i>Lathyrus lanszwertii</i>	Hess 1981 Hess and Wasser 1982 ⁵ Hoffman and Alexander 1975 Hoffman and Alexander 1983 Komarkova 1984 ⁴ Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ³ Wirsing and Alexander 1975 Youngblood 1984 ²
<i>Abies lasiocarpa</i> - <i>Pinus albicaulis</i> / <i>Carex geyseri</i> P.C.	Mountains of southeastern Washington and eastern Oregon	Cool dry	Co-climax with <i>P. albicaulis</i>	<i>P. albicaulis</i> <i>P. engelmannii</i>	<i>C. geyseri</i> <i>L. argenteus</i> <i>Arenaria aculeata</i> <i>A. latifolia</i> <i>V. scoparium</i>	Hall 1973
<i>Abies lasiocarpa</i> / <i>Carex rossii</i> H.T.	Mountains of southern Idaho, Utah, and north- western Wyoming	Warm dry	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. menziesii</i>	<i>C. rossii</i> <i>A. cordifolia</i> <i>Astragalus miser</i> <i>R. woodsii</i>	Steele et al. 1983 Youngblood 1984 ²

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> - <i>Pinus albicaulis</i> H.T.	Mountains of northern Idaho and eastern Washington and Oregon	Cool dry	Co-climax with <i>P. albicaulis</i>	<i>P. albicaulis</i>	<i>V. scoparium</i> <i>X. tenax</i> <i>C. geyseri</i> <i>Luzula glabrata</i>	Daubenmire and Daubenmire 1968
<i>Abies lasiocarpa</i> / <i>Aconitum</i> <i>columbianum</i> H.T.	Mountains of central and southern Utah	Cool moist	Climax	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>A. concolor</i>	<i>A. columbianum</i> <i>Actaea rubra</i> <i>A. cordifolia</i> <i>Bromus ciliatus</i>	Youngblood 1984 ²
<i>Abies lasiocarpa</i> / <i>Actaea rubra</i> H.T.	Mountains of central Idaho, northern Utah, and northwestern Wyoming	Warm moist lower slopes	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. pungens</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>A. rubra</i> <i>O. chilensis</i> <i>L. utahensis</i> <i>V. globulare</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Arnica cordifolia</i> H.T.	Mountains of Montana east of Continental Divide, central Idaho, and northwestern and north-central Wyoming	Cool well- drained	Climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. albicaulis</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>A. cordifolia</i> <i>P. secunda</i> <i>A. miser</i> <i>Fragaria virginiana</i>	Hoffman and Alexander 1976 Komarkova 1984 ⁶ Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Arnica latifolia</i> H.T.	Mountains of southern Idaho, northern Utah, and northwestern Wyoming	Cool dry	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>P. albicaulis</i>	<i>A. latifolia</i> <i>Aster engelmannii</i> <i>Pedicularis racemosa</i>	Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Caltha biflora</i> H.T.	Mountains of central Idaho	Cool wet	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i>	<i>C. biflora</i> <i>Lonicera involucrata</i> <i>Pedicularis bracteosa</i> <i>Dodecatheon jeffreyi</i>	Steele et al. 1981
<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> / <i>Cardamine cordifolia</i> P. C. [<i>A. lasiocarpa</i> / <i>Mertensia</i> <i>ciliata</i> H.T.]	Mountains of central and southern Colorado	Cool wet	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. tremuloides</i>	<i>C. cordifolia</i> <i>Mertensia ciliata</i> <i>Mitella pentandra</i> <i>Carex</i> spp.	DeVelice et al. 1984 ⁶ Steen and Dix 1974 ³
<i>Abies lasiocarpa</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northwestern Montana and northern and central Idaho	Warm moist to cool dry	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. monticola</i>	<i>C. uniflora</i> <i>M. ferruginea</i> <i>V. caespitosum</i> <i>Aralia nudicaulis</i> <i>X. tenax</i>	Cooper et al. 1983 ⁴ Pfister et al. 1977 Steele et al. 1981
<i>Abies lasiocarpa</i> / <i>Coptis occidentalis</i> H.T.	Mountains of northern and central Idaho	Warm well- drained	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>C. occidentalis</i> <i>X. tenax</i> <i>V. globulare</i> <i>M. ferruginea</i>	Cooper et al. 1983 ⁴ Steele et al. 1981
<i>Abies lasiocarpa</i> / <i>Erigeron superbus</i> (<i>E. eximius</i>) H.T.	Mountains of southwest Colorado, northern New Mexico, and Arizona	Cool dry	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>A. concolor</i> <i>P. ponderosa</i> <i>Pinus strobiformis</i> <i>P. tremuloides</i>	<i>E. superbus</i> (<i>E. eximius</i>) <i>Geranium richardsonii</i> <i>Lathyrus arizonicus</i> <i>L. involucrata</i> <i>A. cordifolia</i>	Alexander et al. 1984a DeVelice et al. 1984 ⁶ Fitzhugh et al. 1984 ⁷ Moir and Ludwig 1979
<i>Abies lasiocarpa</i> / <i>Galium triflorum</i> H.T.	Mountains of northern Montana	Warm moist	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>G. triflorum</i> <i>A. rubra</i> <i>Streptopus</i> <i>amplexifolius</i>	Pfister et al. 1977

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies lasiocarpa</i> / <i>Lathyrus arizonicus</i> H.T. [<i>A. lasiocarpa</i> - <i>Pinus</i> <i>stroboformis</i> / <i>L. arizonicus</i> H.T.]	San Francisco, Peaks Arizona; Mogollon Mountains, New Mexico	Cool dry	Climax	<i>P. stroboformis</i> <i>P. tremuloides</i> <i>P. menziesii</i>	<i>L. arizonicus</i> <i>G. richardsonii</i> <i>Smilacina stellata</i> <i>A. glabrum</i> <i>S. oreophilus</i> <i>Vicia americana</i>	Moir and Ludwig 1979 Fitzhugh et al. 1984 ⁷
<i>Abies lasiocarpa</i> - <i>Picea engelmannii</i> / <i>Lupinus argenteus</i> P.C.	Mountains of central and southern Colorado	Warm well- drained	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> (long-lived seral)	<i>L. argenteus</i> <i>V. scoparium</i>	Steen and Dix 1974 ³
<i>Abies lasiocarpa</i> / <i>Osmorhiza chilensis</i> H.T.	Mountains of southern Idaho and northern Utah	Warm moist to well- drained	Climax	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>O. chilensis</i> <i>C. rossii</i> <i>B. repens</i> <i>P. myrsinites</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Pedicularis racemosa</i> H.T.	Mountains of southeast Idaho, northwestern Wyoming, and northern Utah	Warm dry	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>P. racemosa</i> <i>A. cordifolia</i> <i>S. oreophilus</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Polemonium delcatum</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / <i>P.</i> <i>delicatum</i> P.C.	Mountains of central and western Colorado	Cool dry	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>P. delicatum</i> (<i>P. pulcherrimum</i>) <i>Osmorhiza obtusa</i> <i>Vaccinium</i> spp.	Komarkova 1984 ⁸ Steen and Dix 1974 ³
<i>Abies lasiocarpa</i> / <i>Senecio</i> <i>sanguisorboides</i> H.T.	Sacramento Mountains, southern New Mexico	Cool dry to well-drained	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>S. sanguisorboides</i> <i>R. montigenum</i> <i>Ribes wolfii</i>	Alexander et al. 1984a Moir and Ludwig 1979
<i>Abies lasiocarpa</i> / <i>Senecio triangularis</i> H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> <i>S. triangularis</i> H.T. [<i>P. engelmannii</i> / <i>S. triangularis</i> H.T.]	Mountains of north-central and western Colorado	Warm wet stream bottoms	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i>	<i>S. triangularis</i> <i>C. cordifolia</i> <i>Equisetum arvense</i> <i>M. ciliata</i>	Hess 1981 Komarkova 1984 ⁸
<i>Abies lasiocarpa</i> / <i>Streptopus</i> <i>amplexifolius</i> H.T.	Mountains of central Idaho and northwestern Utah	Warm moist to wet	Climax	<i>P. engelmannii</i>	<i>S. amplexifolius</i> <i>S. triangularis</i> <i>Ligusticum canbyi</i> <i>Ribes lacustre</i>	Cooper et al. 1983 ⁴ Steele et al. 1981 Steele et al. 1983
<i>Abies lasiocarpa</i> / <i>Thalictrum occidentale</i> H.T.	Mountains of southeastern Idaho and north- western Wyoming	Warm well- drained	Climax	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>T. occidentale</i> <i>O. chilensis</i> <i>A. cordifolia</i>	Steele et al. 1983
<i>Abies lasiocarpa</i> / Moss spp. H.T. <i>A. lasiocarpa</i> - <i>Picea</i> <i>engelmannii</i> / Moss spp. P.C.	Mountains of central, and southwestern Colorado, and northern New Mexico	Cool dry to well-drained	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. aristata</i> <i>P. tremuloides</i> <i>P. contorta</i>	Moss spp. <i>V. caespitosum</i> <i>Rosa</i> spp.	DeVelice et al. 1984 ⁶ Komarkova 1984 ⁸ Steen and Dix 1974 ³
<i>Abies lasiocarpa</i> / Scree H.T.	Mountains of northern New Mexico and southern Colorado	Warm dry	Climax	<i>P. menziesii</i> <i>P. stroboformis</i>	<i>S. oreophilus</i> <i>J. communis</i> <i>Holodiscus dumosus</i> <i>L. involucreta</i> <i>Erigeron vetensis</i>	DeVelice et al. 1984 ⁶ Fitzhugh et al. 1984 ⁷

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority'
<i>Picea engelmannii</i> series						
<i>Picea engelmannii</i> / <i>Acer glabrum</i>	Sacramento Mountains, New Mexico; Chiricahua Mountains, Arizona	Warm moist	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. tremuloides</i>	<i>A. glabrum</i> <i>B. ciliatus</i> <i>Viola canadensis</i> <i>S. stellata</i>	Alexander et al. 1984a Moir and Ludwig 1979
<i>Picea engelmannii</i> / <i>Physocarpus malvaceus</i> H.T.	Mountains of south-central Montana	Warm moist	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>P. malvaceus</i> <i>S. albus</i> <i>S. betulifolia</i>	Pfister et al. 1977
<i>Picea engelmannii</i> / <i>Vaccinium myrtillus</i> H.T.	Sangre de Cristo Mountains, south- ern Colorado and northern New Mexico	Cool dry	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. tremuloides</i> <i>P. aristata</i>	<i>V. myrtillus</i> <i>P. delicatum</i> (<i>P. pulcherrimum</i>) <i>Senecio</i> spp. <i>Deschampsia</i> <i>caespitosa</i> <i>Poa reflexa</i>	DeVelice et al. 1984 ^a Fitzhugh et al. 1984 ⁷ Moir and Ludwig 1979
[<i>P. engelmannii</i> / <i>V. myrtillus</i> - <i>Polemonium</i> <i>pulcherrimum</i> H.T.] <i>P. engelmannii</i> / <i>Vaccinium scoparium</i> - <i>P. delicatum</i> H.T.]						
<i>Picea engelmannii</i> / <i>Vaccinium scoparium</i> H.T.	Mountains of northwestern Wyoming	Cool dry	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. flexilis</i> <i>P. albicaulis</i>	<i>V. scoparium</i> <i>A. cordifolia</i> <i>Antennaria</i> spp. <i>Lupinus</i> spp.	Steele et al. 1983
<i>Picea engelmannii</i> / <i>Elymus triticoides</i> H.T.	Capitan Mountains, New Mexico	Cool dry to well-drained	Minor climax to or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i>	<i>E. triticoides</i> <i>A. glabrum</i> <i>Jamesia americana</i>	Alexander et al. 1984a Moir and Ludwig 1979
<i>Picea engelmannii</i> / <i>Carex disperma</i> H.T.	Mountains of central and southern Idaho and western Wyoming	Cool moist	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. pungens</i>	<i>C. disperma</i> <i>P. secunda</i> <i>G. triflorum</i>	Steele et al. 1981 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Caltha leptosepala</i> H.T.	Mountains of northwestern Wyoming and east- central Idaho	Warm moist	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i>	<i>C. leptosepala</i> <i>Trollius taxus</i>	Steele et al. 1983
<i>Picea engelmannii</i> / <i>Equisetum arvense</i> H.T.	Mountains of southern Montana, northwestern Wyoming, central Idaho, and northern Utah	Warm to cool, wet	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. pungens</i>	<i>E. arvense</i> <i>S. amplexifolius</i> <i>S. triangularis</i> <i>Luzula parviflora</i>	Mauk and Henderson 1984 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Galium trifolium</i> H.T.	Mountains of central Idaho and northwestern Wyoming	Warm moist	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. pungens</i>	<i>G. trifolium</i> <i>A. rubra</i> <i>S. stellata</i> <i>S. amplexifolius</i>	Steele et al. 1981 Steele et al. 1983
<i>Picea engelmannii</i> / <i>Senecio cardamine</i> H.T.	Blue Mountains, Arizona	Cool moist	Seral to <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. pungens</i> <i>Pinus ponderosa</i> <i>P. strobiformis</i> <i>A. concolor</i> <i>P. tremuloides</i>	<i>S. cardamine</i> <i>Fragaria ovalis</i> <i>G. richardsonii</i> <i>V. canadensis</i>	Fitzhugh et al. 1984 ⁷
<i>Picea engelmannii</i> / <i>Trifolium dasyphyllum</i> H.T.	Mountains of north-central Colorado	Cold dry	Minor climax to or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. tremuloides</i>	<i>T. dasyphyllum</i> <i>Pyrola chlorantha</i> <i>Sedum lanceolatum</i>	Hess 1981
<i>Picea engelmannii</i> / Moss spp. H.T.	Mountains of northern New Mexico	Cool dry to well-drained	Co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. aristata</i> <i>P. tremuloides</i> <i>P. menziesii</i>	Moss spp. <i>Ribes</i> spp. <i>Vaccinium</i> spp. <i>L. arizonicus</i>	Alexander et al. 1984b ¹ Fitzhugh et al. 1984 ⁷ Moir and Ludwig 1979

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Picea engelmannii</i> / Scree H.T.	Mountains of northern New Mexico and southern Colorado	Warm dry	Minor climax to <i>P. engelmannii</i>	<i>P. engelmannii</i>	<i>J. communis</i> <i>Saxifrage</i> <i>bronchialis</i>	DeVelice et al. 1984 ^a
<i>Picea pungens</i> series						
<i>Picea pungens</i> / <i>Amelanchier alnifolia</i> H.T.	Mountains of central and western Colorado	Warm moist	Minor climax to <i>P. pungens</i>	<i>P. pungens</i> <i>P. menziesii</i> <i>Populus angustifolia</i>	<i>A. alnifolia</i> <i>Cornus stolonifera</i> <i>C. geyeri</i> <i>Swida sericea</i>	Hess and Wasser 1982 ^b Komarkova 1984 ^a
<i>Picea pungens</i> / <i>Erigeron eximus</i> H.T. [<i>P. pungens</i> - <i>Picea</i> <i>engelmannii</i> / <i>E.</i> <i>superbus</i> H.T.]	White Mountains, Arizona	Cool dry	Minor climax to <i>P. engelmannii</i> <i>P. pungens</i>	<i>P. pungens</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>P. strobiformis</i> <i>P. tremuloides</i> <i>P. concolor</i>	<i>E. superbus</i> (<i>E. eximus</i>) <i>Festuca arizonica</i> <i>Carex foenea</i> <i>F. virginiana</i>	Moir and Ludwig 1979
<i>Picea pungens</i> / <i>Senecio cardamine</i> H.T. [<i>P. pungens</i> - <i>Picea</i> <i>engelmannii</i> / <i>S.</i> <i>cardamine</i> H.T.]	White Mountains, Arizona	Cool moist	Co-climax with or minor climax to <i>P. engelmannii</i> <i>P. pungens</i>	<i>P. engelmannii</i> <i>P. pungens</i> <i>P. ponderosa</i> <i>P. menziesii</i> <i>P. strobiformis</i> <i>P. tremuloides</i> <i>A. concolor</i>	<i>S. cardamine</i> <i>Pteridium aquilinum</i> <i>Helenium hoopesii</i> <i>V. canadensis</i>	Fitzhugh et al. 1984 ^c Moir and Ludwig 1979
<i>Pinus contorta</i> series and other <i>P. contorta</i> dominated vegetation						
<i>Pinus contorta</i> / <i>Alnus crispa</i> P.C.	Mountains of Alberta and southern British Columbia	Cool moist to well- drained	Co-climax with <i>Picea glauca</i> <i>P. engelmannii</i>	<i>P. glauca</i> <i>P. engelmannii</i> <i>P. contorta</i>	<i>A. crispa</i> <i>Cornus canadensis</i> <i>A. uva-ursi</i> <i>L. borealis</i> <i>A. cordifolia</i> <i>Vaccinium</i> <i>myrtilloides</i>	Corns 1978 Corns and LaRoi 1976 LaRoi and Hnatiuk 1980 Wali and Krajina 1973
<i>Pinus contorta</i> / <i>Arctostaphylos uva-</i> <i>ursi</i> H.T.(UT); P.C.(CO)	Uinta Mountains, Utah; mountains of central Colorado.	Warm dry	Minor climax to <i>P. contorta</i> (UT); ultimate climax unknown (CO); probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>A. uva-ursi</i> <i>B. repens</i> <i>Sitanion hystrix</i>	Mauk and Henderson 1984 Steen and Dix 1974 ^d
<i>Pinus contorta</i> / <i>Juniperus communis</i> H.T.(CO); C.T.(ID,WY)	Mountains of eastern Idaho, northwestern Wyoming, and central Colorado	Warm dry	Minor climax to <i>P. contorta</i> (CO); ultimate climax unknown (ID,WY), probably co-climax with <i>P. engelmannii</i> <i>P. menziesii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>P. albicaulis</i> <i>P. contorta</i>	<i>J. communis</i> <i>A. uva-ursi</i> <i>S. canadensis</i> <i>A. cordifolia</i>	Hess 1981 Steele et al. 1983
<i>Pinus contorta</i> / <i>Ledum groenlandicum</i> P.C.	Mountains of Alberta	Cool moist	Minor climax to <i>P. engelmannii</i> <i>P. glauca</i> <i>Picea mariana</i>	<i>P. engelmannii</i> <i>P. glauca</i> <i>P. mariana</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>L. groenlandicum</i> <i>V. scoparium</i> <i>C. canadensis</i> <i>V. membranaceum</i>	Corns 1978 Corns and LaRoi 1976 LaRoi and Hnatiuk 1980
<i>Pinus contorta</i> / <i>Linnaea borealis</i> C.T. (MT, WY); P.C.(CO)	Mountains of Montana east of Continental Divide, northwestern Wyoming, and central Colorado	Cool moist to well- drained	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>L. borealis</i> <i>V. scoparium</i> <i>V. globulare</i> <i>A. cordifolia</i> <i>C. rubescens</i>	Pfister et al. 1977 Steele et al. 1983 Steen and Dix 1974 ^d
<i>Pinus contorta</i> / <i>Menziesia glabella</i> P.C.	Mountains of Alberta	Cool moist	Co-climax with <i>P. glauca</i> <i>P. engelmannii</i> <i>P. menziesii</i>	<i>P. glauca</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>M. glabella</i> <i>V. scoparium</i> <i>Rubus pedatus</i> <i>L. borealis</i> <i>C. canadensis</i>	Corns 1978 LaRoi and Hnatiuk 1980

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus contorta</i> / <i>Pachistima myrsinites</i> P.C.	Mountains of central Colorado	Warm dry to well- drained	Ultimate climax unknown; probably climax or co- climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. tremuloides</i> <i>P. contorta</i>	<i>P. myrsinites</i> <i>V. scoparium</i> <i>J. communis</i> <i>L. borealis</i>	Steen and Dix 1974 ³
<i>Pinus contorta</i> / <i>Purshia tridentata</i> H.T.; C.T.	Mountains of southern Washing- ton, northern and central Oregon, and western Montana	Cool-warm dry to well- drained	Minor climax to <i>P. contorta</i> (RM) Seral to <i>P. contorta</i> (PNW)	<i>P. contorta</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>P. ponderosa</i>	<i>P. tridentata</i> <i>A. uva-ursi</i> <i>C. rossii</i> <i>Ribes cereum</i> <i>Festuca idahoensis</i> <i>Epilobium</i> <i>angustifolium</i> <i>Stipa occidentalis</i> <i>Carex pensylvanica</i>	Pfister et al. 1977 Volland 1976 Youngberg and Dalms 1970
<i>Pinus contorta</i> / <i>Shepherdia canadensis</i> C.T.; P.C.	Mountains of southern British Columbia and Alberta, south- eastern Idaho, northwestern Wyoming, and central Colorado	Cool-warm dry to well- drained	Ultimate climax unknown; probably climax or co- climax with <i>P. engelmannii</i> <i>P. glauca</i>	<i>P. glauca</i> <i>P. engelmannii</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>S. canadensis</i> <i>A. cordifolia</i> <i>J. communis</i> <i>L. borealis</i> <i>A. uva-ursi</i>	LaRoi and Hnatiuk 1980 Steen and Dix 1974 ³ Steele et al. 1983 Wali and Krajina 1973
<i>Pinus contorta</i> / <i>Spiraea betulifolia</i> C.T.	Mountains of eastern Idaho and northwestern Wyoming	Warm dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. tremuloides</i> <i>P. contorta</i>	<i>S. betulifolia</i> <i>C. rubescens</i> <i>C. geyeri</i>	Steele et al. 1983
<i>Pinus contorta</i> / <i>Spiraea lucida</i> P.C.	Mountains of Alberta east of Continental Divide	Cold moist	Minor climax to <i>P. engelmannii</i> <i>P. mariana</i>	<i>P. engelmannii</i> <i>P. mariana</i> <i>P. contorta</i>	<i>S. lucida</i> <i>L. borealis</i> (codom) <i>C. rubescens</i>	Thompson and Kuist 1976
<i>Pinus contorta</i> / <i>Symphoricarpos albus</i> P.C.	Mountains of southwestern Alberta	Warm well- drained	Co-climax with <i>P. glauca</i> <i>P. menziesii</i> <i>P. engelmannii</i>	<i>P. glauca</i> <i>P. menziesii</i> <i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>S. albus</i> <i>A. cordifolia</i> <i>L. borealis</i>	Kuchar 1973
<i>Pinus contorta</i> / <i>Vaccinium caespitosum</i> C.T.	Mountains of eastern Montana, Idaho, and northern Utah	Cool well- drained	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>V. caespitosum</i> <i>V. scoparium</i> <i>Festuca ovina</i> <i>L. borealis</i>	Cooper et al. 1983 ⁴ Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981
<i>Pinus contorta</i> / <i>Vaccinium globulare</i> C.T.	Mountains of southern Idaho, northwestern Wyoming, and northern Utah	Cool well- drained	Ultimate climax unknown; probably climax or co- climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>V. globulare</i> <i>L. utahensis</i> <i>V. scoparium</i> <i>C. rubescens</i>	Steele et al. 1983
<i>Pinus contorta</i> / <i>Vaccinium</i> <i>membranaceum</i> P.C.	Mountains of southern British Columbia	Cool moist	Minor climax to <i>P. engelmannii</i> <i>P. glauca</i>	<i>P. engelmannii</i> <i>P. glauca</i> <i>A. lasiocarpa</i> <i>P. contorta</i>	<i>V. membranaceum</i> <i>C. canadensis</i> (codom) <i>C. uniflora</i> <i>L. borealis</i>	Wali and Krajina 1973
<i>Pinus contorta</i> / <i>Vaccinium myrtilloides</i> P.C.	Foothills of western Alberta	Warm dry to moist	Minor climax to <i>P. glauca</i> <i>P. engelmannii</i>	<i>P. glauca</i> <i>P. engelmannii</i> <i>P. contorta</i>	<i>V. myrtilloides</i> <i>Cladonia</i> spp. (codom)	Corns 1978

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus contorta</i> / <i>Vaccinium scoparium</i> C.T.; P.C.(OR,WA)	Mountains of Montana, central Idaho, north- western Wyoming, northern Utah southern Wyoming and central Colorado; moun- tains of central and eastern Oregon, and southeastern Washington	Cool to cold dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i> <i>P. menziesii</i> (RM); seral to <i>Tsuga</i> <i>mertensiana</i> (PNW)	<i>P. menziesii</i> <i>P. engelmannii</i> <i>T. mertensiana</i> <i>P. albicaulis</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. flexilis</i> <i>Abies grandis</i> <i>Tsuga heterophylla</i> <i>L. occidentalis</i>	<i>V. scoparium</i> <i>C. rubescens</i> <i>A. cordifolia</i> <i>L. argenteus</i> <i>B. repens</i> <i>C. geyeri</i> <i>R. cereum</i>	Cooper et al. 1983 ⁴ Hall 1973 Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ³ Wirsing and Alexander 1975 Volland 1976 Youngberg and Dahms 1970
<i>Pinus contorta</i> / <i>Viburnum edule</i> P.C.	Foothills of western Alberta	Warm moist	Minor climax to <i>P. glauca</i> <i>P. engelmannii</i>	<i>P. glauca</i> <i>P. engelmannii</i> <i>P. contorta</i>	<i>V. edule</i> <i>Rubus pubescens</i> (codom)	LaRoi and Hnatiuk 1980
<i>Pinus contorta</i> / <i>Xerophyllum tenax</i> C.T.(ID); P.C.(OR)	Mountains of central Oregon and northern Idaho	Warm dry	Co-climax with <i>T. mertensiana</i> (OR) ultimate climax unknown (ID)	<i>T. mertensiana</i> (OR) <i>P. monticola</i> (OR) <i>P. contorta</i> <i>P. engelmannii</i> (ID) <i>P. menziesii</i> (ID)	<i>X. tenax</i> <i>C. pensylvanica</i> (OR) <i>L. argenteus</i> (OR) <i>Vaccinium</i> spp. (ID)	Cooper et al. 1983 ⁴ Volland 1976
<i>Pinus contorta</i> / <i>Calamagrostis</i> <i>canadensis</i> C.T.	Uinta Mountains, Utah	Cool moist	Ultimate climax unknown; probably climax or co- climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i>	<i>C. canadensis</i> <i>A. cordifolia</i> <i>J. communis</i> <i>Poa nervosa</i>	Mauk and Henderson 1984
<i>Pinus contorta</i> / <i>Calamagrostis</i> <i>rubescens</i> C.T.	Mountains of eastern Washing- ton and Oregon, Montana, Idaho, northeastern Utah, and northwestern Wyoming	Warm dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i> , except minor climax to <i>A. grandis</i> in the Blue Mountains	<i>P. engelmannii</i> <i>A. menziesii</i> <i>P. grandis</i> <i>P. contorta</i> <i>L. occidentalis</i> <i>P. tremuloides</i>	<i>C. rubescens</i> <i>V. scoparium</i> <i>C. geyeri</i> <i>A. cordifolia</i> <i>A. uva-ursi</i>	Hall 1973 Pfister et al. 1977 Steele et al. 1983
<i>Pinus contorta</i> / <i>Carex geyeri</i> C.T. (ID,WY) P.C.(CO)	Mountains of central Idaho, northwestern Wyoming, southern Wyoming, and central Colorado	Cool dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. flexilis</i> <i>P. tremuloides</i>	<i>C. geyeri</i> <i>S. oreophilus</i> <i>A. cordifolia</i> <i>L. argenteus</i> <i>B. repens</i> <i>J. communis</i>	Hess 1981 Hess and Wasser 1982 ⁵ Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974 ³ Wirsing and Alexander 1975
<i>Pinus contorta</i> / <i>Carex rossii</i> C.T.	Mountains of northwestern Wyoming	Warm dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. albicaulis</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>C. rossii</i> <i>L. argenteus</i> <i>P. nervosa</i>	Steele et al. 1983
<i>Pinus contorta</i> / <i>Arnica cordifolia</i> C.T.	Mountains of eastern Idaho and northwestern Wyoming	Cool dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. albicaulis</i> <i>P. flexilis</i>	<i>A. cordifolia</i> <i>Antennaria racemosa</i> <i>A. miser</i> <i>P. secunda</i>	Steele et al. 1983
<i>Pinus contorta</i> / <i>Lupinus argenteus</i> P.C.	Mountains of central and southern Colorado	Warm dry to well- drained	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. tremuloides</i> <i>P. contorta</i>	<i>L. argenteus</i>	Steen and Dix 1974 ³

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Pinus contorta</i> Lichen spp. P.C.	Mountains of central Colorado	Hot dry	Ultimate climax unknown; probably climax	<i>P. contorta</i> <i>P. tremuloides</i>	Lichen spp.	Steen and Dix 1974 ³
Populus tremuloides series and other <i>P. tremuloides</i> dominated vegetation						
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Berberis repens</i> C.T. <i>P. tremuloides</i> / <i>B. repens</i> C.T.	Mountains of western Wyoming	Warm to cool. Well- drained	Climax or co- climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. ponderosa</i> <i>P. glauca</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>B. repens</i> <i>S. albus</i> <i>P. myrsinites</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> / <i>Pachistima myrsinites</i> C.T.(ID); P.C.(CO)	Mountains of southeastern Idaho and central and southwestern Colorado	Warm dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i> <i>P. menziesii</i>	<i>P. myrsinites</i> <i>V. scoparium</i> <i>C. geyeri</i> <i>C. rubescens</i>	Mueggler and Campbell 1982 Steen and Dix 1974 ³
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Prunus virginiana</i> C.T. <i>P. tremuloides</i> / <i>P. virginiana</i> C.T.	Mountains of western Wyoming	Warm dry	Climax or co- climax with <i>P. menziesii</i>	<i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>P. virginiana</i> <i>B. repens</i> <i>S. oreophilus</i> <i>R. woodsii</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Shepherdia canadensis</i> C.T. <i>P. tremuloides</i> / <i>S. canadensis</i> C.T.	Mountains of western Wyoming	Cool-dry to well- drained	Climax	<i>P. contorta</i> <i>P. tremuloides</i>	<i>S. canadensis</i> Geranium <i>viscosissimum</i> <i>A. cordifolia</i> <i>R. woodsii</i> <i>T. fendleri</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Symphoricarpos</i> <i>oreophilus</i> C.T. <i>P. tremuloides</i> / <i>S. oreophilus</i> C.T.	Mountains of southeastern Idaho, northern Utah, and western Wyoming	Warm well- drained	Ultimate climax unknown; probably climax or co-climax with <i>P. menziesii</i> <i>A. lasiocarpa</i>	<i>A. lasiocarpa</i> <i>P. menziesii</i> <i>A. concolor</i> <i>P. tremuloides</i>	<i>S. oreophilus</i> <i>P. virginiana</i> <i>B. repens</i> <i>Elymus glaucus</i> <i>C. rubescens</i>	Mauk and Henderson 1984 Mueggler and Campbell 1982 Steele et al. 1983 Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Pseudotsuga menziesii</i> / <i>Symphoricarpos</i> <i>oreophilus</i> C.T. <i>P. tremuloides</i> / <i>S. oreophilus</i> C.T.	Mountains of southeastern Idaho	Warm dry	Ultimate climax unknown; probably minor climax to <i>P. menziesii</i>	<i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>S. oreophilus</i> <i>C. rubescens</i> <i>Poa pratensis</i> <i>C. geyeri</i>	Mueggler and Campbell 1982
<i>Populus tremuloides</i> - <i>Pinus contorta</i> / <i>Calamagrostis</i> <i>rubescens</i> C.T. <i>P. tremuloides</i> <i>C. rubescens</i> C.T.	Mountains of southeastern Idaho	Warm dry	Ultimate climax unknown; probably climax or co-climax with <i>P. menziesii</i>	<i>P. menziesii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>C. rubescens</i> <i>S. oreophilus</i> <i>P. myrsinites</i> <i>L. argenteus</i> <i>T. fendleri</i> <i>G. viscosissimum</i>	Mueggler and Campbell 1982
<i>Populus tremuloides</i> / <i>Elymus glaucus</i> P.C.	Mountains of central and southwestern Colorado	Warm moist to well- drained	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>E. glaucus</i> <i>A. alnifolia</i> <i>Symphoricarpos</i> spp. <i>Ligusticum porteri</i>	Steen and Dix 1974 ³
<i>Populus tremuloides</i> / <i>Festuca thurberi</i> P.C.	Mountains of southwestern Colorado	Warm dry	Ultimate climax unknown; probably climax or co-climax with <i>P. engelmannii</i>	<i>P. engelmannii</i> <i>P. tremuloides</i> <i>P. menziesii</i> <i>P. flexilis</i>	<i>F. thurberi</i> <i>B. repens</i> <i>S. oreophilus</i> <i>F. ovalis</i>	Steen and Dix 1974 ³
<i>Populus tremuloides</i> / <i>Poa pratensis</i> C.T.	Mountains of southeastern Idaho	Warm dry	Ultimate climax unknown; probably climax or co-climax with <i>P. menziesii</i>	<i>P. menziesii</i> <i>P. tremuloides</i>	<i>P. pratensis</i> <i>C. rubescens</i> <i>T. fendleri</i> <i>P. nervosa</i> <i>L. argenteus</i>	Mueggler and Campbell 1982

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Arnica cordifolia</i> C.T. <i>P. tremuloides</i> / <i>A. cordifolia</i> C.T.	Mountains of western Wyoming	Cool moist to well- drained	Climax	<i>P. contorta</i> <i>P. tremuloides</i>	<i>A. cordifolia</i> <i>S. oreophilus</i> <i>C. rossii</i> <i>O. chilensis</i> <i>P. nervosa</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> / <i>Geranium</i> <i>viscosissimum</i> C.T.	Mountains of southeastern Idaho	Warm dry	Climax	<i>P. tremuloides</i>	<i>G. viscosissimum</i> <i>Symphoricarpos</i> spp. <i>L. argenteus</i> <i>T. fendleri</i>	Mueggler and Campbell 1982
<i>Populus tremuloides</i> / <i>Heracleum lanatum</i> C.T.	Mountains of western Wyoming	Warm moist	Climax	<i>P. engelmannii</i> <i>P. contorta</i> <i>P. tremuloides</i>	<i>H. lanatum</i> <i>P. bracteosa</i> <i>T. fendleri</i> <i>E. glaucus</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Ligusticum filicinum</i> C.T. <i>P. tremuloides</i> / <i>L. filicinum</i> C.T.	Mountains of western Wyoming	Cool moist to well- drained	Climax	<i>P. menziesii</i> <i>P. flexilis</i> <i>P. tremuloides</i>	<i>L. filicinum</i> <i>T. fendleri</i> <i>G. viscosissimum</i> <i>Osmorhiza</i> <i>occidentalis</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Pedicularis racemosa</i> C.T.	Mountains of western Wyoming	Cool moist	Climax	<i>P. engelmannii</i> <i>P. tremuloides</i>	<i>P. racemosa</i> <i>A. cordifolia</i> <i>S. oreophilus</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> / <i>Ranunculus</i> <i>alismaefolius</i> C.T.	Mountains of western Wyoming	Cool moist to wet	Climax	<i>P. engelmannii</i> <i>P. tremuloides</i>	<i>R. alismaefolius</i> <i>Carex microptera</i> <i>Trifolium longipes</i>	Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Rudbeckia</i> <i>occidentalis</i> C.T. <i>P. tremuloides</i> / <i>R. occidentalis</i> C.T.	Mountains of southeastern Idaho and western Wyoming	Cool moist to well- drained	Climax	<i>P. engelmannii</i> <i>P. tremuloides</i>	<i>R. occidentalis</i> <i>T. longipes</i> <i>Nemophila</i> <i>breviflora</i> <i>Melica spectabilis</i> <i>Symphoricarpos</i> spp.	Mueggler and Campbell 1982 Youngblood and Mueggler 1981
<i>Populus tremuloides</i> - <i>Abies lasiocarpa</i> / <i>Thalictrum fendleri</i> C.T.	Mountains of southeastern Idaho	Warm moist	Climax	<i>P. tremuloides</i>	<i>T. fendleri</i> <i>S. oreophilus</i> <i>G. viscosissimum</i> <i>O. chilensis</i>	Mueggler and Campbell 1982
<i>Pseudotsuga menziesii</i> series						
<i>Pseudotsuga menziesii</i> / <i>Arctostaphylos</i> <i>uva-ursi</i> H.T.	Mountains of southwestern New Mexico	Warm dry	Minor climax to <i>P. menziesii</i>	<i>P. menziesii</i> <i>P. ponderosa</i> <i>P. tremuloides</i> <i>P. strobiformis</i> <i>P. flexilis</i> <i>P. engelmannii</i>	<i>A. uva-ursi</i> <i>A. spicatum</i> <i>Festuca</i> spp. <i>B. sagittata</i> <i>Lithospermum ruderales</i>	Fitzhugh et al. 1984 ⁷
<i>Pseudotsuga menziesii</i> / Scree H.T.	Mountains of New Mexico	Warm dry	Seral to <i>P. menziesii</i>	<i>P. menziesii</i> <i>P. engelmannii</i> <i>P. tremuloides</i> <i>P. strobiformis</i>	<i>Salix</i> spp. <i>S. oreophilus</i> <i>H. dumosus</i> <i>B. ciliatus</i>	DeVelice et al. 1984 ⁸ Fitzhugh et al. 1984 ⁷
<i>Thuja plicata</i> series						
<i>Thuja plicata</i> / <i>Oplopanax horridum</i> H.T.	Mountains of northwestern Montana and southern British Columbia	Warm wet to cool wet	Seral or minor climax to <i>T. plicata</i>	<i>T. plicata</i> <i>T. heterophylla</i> <i>T. mertensiana</i> <i>P. monticola</i> <i>Abies amabilis</i>	<i>O. horridum</i> <i>Athyrium</i> <i>filix-femina</i> <i>Gymnocarpium</i> <i>dryopteris</i>	Brooke et al. 1970 Pfister et al. 1977
<i>Thuja plicata</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northwestern Montana and northern Idaho	Cool to warm dry, bottom- lands	Seral or minor climax to <i>T. plicata</i>	<i>T. plicata</i> <i>A. grandis</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. contorta</i>	<i>C. uniflora</i> <i>M. ferruginea</i> <i>A. nudicaulis</i> <i>X. tenax</i>	Cooper et al. 1983 ⁴ Pfister et al. 1977

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
Abies grandis series						
<i>Abies grandis</i> / <i>Acer glabrum</i> H.T.	Mountains of central Idaho	Warm moist	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. contorta</i> <i>P. menziesii</i>	<i>A. glabrum</i> <i>P. malvaceus</i>	Steele et al. 1981
<i>Abies grandis</i> / <i>Linnaea borealis</i> H.T.	Mountains of central Montana	Cool moist to well- drained	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. contorta</i> <i>P. engelmannii</i> <i>P. monticola</i> <i>P. ponderosa</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>L. borealis</i> <i>Adenocaulon bicolor</i> <i>Disporum hookeri</i>	Pfister et al. 1977
<i>Abies grandis</i> / <i>Vaccinium caespitosum</i> H.T.	Mountains of central Idaho	Cool well- drained	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>V. caespitosum</i> <i>F. virginiana</i> <i>C. rubescens</i>	Steele et al. 1981
<i>Abies grandis</i> / <i>Vaccinium globulare</i> H.T.	Mountains of central Idaho	Cool well- drained	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i>	<i>V. globulare</i>	Steele et al. 1981
<i>Abies grandis</i> / <i>Xerophyllum tenax</i> H.T.	Mountains of northern Idaho	Cool dry	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. engelmannii</i> <i>P. contorta</i> <i>P. ponderosa</i> <i>P. menziesii</i>	<i>X. tenax</i> <i>V. globulare</i>	Cooper et al. 1983 ^a
<i>Abies grandis</i> / <i>Clintonia uniflora</i> H.T.	Mountains of western Montana and northern Idaho	Warm moist	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. menziesii</i> <i>P. engelmannii</i> <i>L. occidentalis</i> <i>P. contorta</i> <i>P. ponderosa</i>	<i>C. uniflora</i> <i>L. borealis</i> <i>A. bicolor</i> <i>X. tenax</i> <i>M. ferruginea</i>	Cooper et al. 1983 ^a Pfister et al. 1977
<i>Abies grandis</i> / <i>Coptis occidentalis</i> H.T.	Mountains of northern Idaho	Warm moist	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. engelmannii</i> <i>P. contorta</i> <i>P. ponderosa</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>C. occidentalis</i> <i>V. globulare</i> <i>X. tenax</i> <i>S. albus</i>	Cooper et al. 1983 ^a
<i>Abies grandis</i> / <i>Senecio triangularis</i> H.T.	Mountains of northern Idaho	Warm moist	Minor climax to <i>A. grandis</i>	<i>A. grandis</i> <i>P. engelmannii</i> <i>L. occidentalis</i>	<i>S. triangularis</i> <i>A. filix-femina</i> <i>Trautvetteria</i> <i>caroliniensis</i>	Cooper et al. 1983 ^a
Abies concolor series						
<i>Abies concolor</i> / <i>Vaccinium myrtillus</i> H.T.	Mountains of northern New Mexico and southern Colorado	Cool dry	Minor climax to <i>A. concolor</i> <i>P. menziesii</i>	<i>A. concolor</i> <i>P. menziesii</i> <i>P. pungens</i> <i>P. engelmannii</i> <i>P. tremuloides</i>	<i>V. myrtillus</i> <i>A. uva-ursi</i> <i>P. myrsinites</i> <i>A. glabrum</i> <i>R. paviflorus</i>	DeVelice et al. 1984 ^b
Abies amabilis series						
<i>Abies amabilis</i> / <i>Menziesia ferruginea</i> P.C.	Central Cascades, Oregon and Washington	Cool moist	Seral to <i>A. amabilis</i>	<i>A. amabilis</i> <i>T. mertensiana</i> <i>Chamaecyparis</i> <i>nootkatensis</i>	<i>M. ferruginea</i> <i>V. membranaceum</i>	Franklin 1966
<i>Abies amabilis</i> - <i>Tsuga mertensiana</i> / <i>Xerophyllum tenax</i> P.C.	Western Cascades, central Oregon	Warm dry	Seral to <i>A. amabilis</i> <i>T. mertensiana</i>	<i>A. amabilis</i> <i>T. mertensiana</i> <i>P. contorta</i>	<i>X. tenax</i> <i>V. membranaceum</i>	Franklin and Dyrness 1973
<i>Abies amabilis</i> / <i>Streptopus roseus</i> P.C.	Mountains of southern British Columbia	Cool wet	Seral to <i>A. amabilis</i>	<i>A. amabilis</i> <i>T. mertensiana</i> <i>C. nootkatensis</i>	<i>S. roseus</i>	Brooke et al. 1970

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Abies amabilis</i> / <i>Veratrum viride</i> P.C.	Cascades, southern Washington and northern Oregon	Cool wet	Seral to <i>A. amabilis</i>	<i>A. amabilis</i> <i>T. mertensiana</i> <i>P. menziesii</i>	<i>V. viride</i>	Franklin 1966
<i>Abies magnifica</i> series						
<i>Abies magnifica</i> / <i>Leucothoe davisiae</i> P.C.	Russian Peak, Kalmath Mountains, California	Cool wet	Minor climax to <i>A. amabilis</i> <i>A. magnifica</i>	<i>A. magnifica</i> <i>A. amabilis</i> <i>A. concolor</i> <i>Pinus lambertiana</i> <i>P. engelmannii</i> (minor climax) <i>Picea brewerana</i> <i>P. monticola</i> <i>Taxus brevifolia</i> <i>T. mertensiana</i> <i>Libocedrus decurrens</i>	<i>L. davisiae</i> <i>R. lacustre</i> <i>Alnus tenuifolia</i> <i>Sorbus californica</i>	Sawyer and Thornburgh 1977
<i>Abies magnifica</i> / <i>Linnaea borealis</i> P.C.	Russian Peak, Klamath Mountains, California	Cool moist open	Minor climax to <i>A. magnifica</i>	<i>A. magnifica</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. ponderosa</i> <i>P. engelmannii</i> <i>P. monticola</i> <i>T. mertensiana</i> <i>A. concolor</i> <i>P. lambertiana</i> <i>A. amabilis</i>	<i>L. borealis</i> <i>Poa secunda</i> <i>Anemone deltoidea</i> <i>Chimaphila umbellata</i>	Sawyer and Thornburgh 1977
<i>Tsuga heterophylla</i> series						
<i>Tsuga heterophylla</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northwestern Montana and northern Idaho	Warm moist	Minor climax to <i>T. heterophylla</i> <i>T. plicata</i>	<i>T. heterophylla</i> <i>T. plicata</i> <i>P. monticola</i> <i>P. contorta</i> <i>P. menziesii</i> <i>L. occidentalis</i> <i>P. engelmannii</i>	<i>C. uniflora</i> <i>A. nudicaulis</i> <i>X. tenax</i> <i>M. ferruginea</i>	Cooper et al. 1983* Pfister et al. 1977
<i>Tsuga mertensiana</i> series						
<i>Tsuga mertensiana</i> / <i>Cladanthamnus</i> <i>pyrolaeflorus</i> P.C.	Mountains of southern British Columbia	Cool dry	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. amabilis</i> <i>P. menziesii</i>	<i>C. pyrolaeflorus</i> <i>V. membranaceum</i>	Brooke et al. 1970
<i>Tsuga mertensiana</i> / <i>Menziesia ferruginea</i> H.T.	Mountains of southern Washington, northern Idaho, and western Montana; mountains of British Columbia to central Oregon	Cool moist	Minor climax to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. engelmannii</i> <i>L. occidentalis</i> <i>P. contorta</i> <i>A. amabilis</i>	<i>M. ferruginea</i> <i>R. albiflorum</i> <i>X. tenax</i> <i>L. hitchcockii</i>	Brockway et al. 1983 Cooper et al. 1983* Daubenmire and Daubenmire 1968 Pfister et al. 1977
<i>Tsuga mertensiana</i> / <i>Rhododendron</i> <i>albiflorum</i> P.C.	Mountains of southern Washington	Cool moist	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. engelmannii</i> <i>T. heterophylla</i> <i>A. amabilis</i> <i>C. nootkatensis</i>	<i>R. albiflorum</i> <i>M. ferruginea</i> <i>Vaccinium</i> spp. <i>P. secunda</i>	Brockway et al. 1983
<i>Tsuga mertensiana</i> - <i>Abies amabilis</i> / <i>Vaccinium alaskaense</i> P.C.	Mountains of southern British Columbia	Cool moist	Seral to <i>T. mertensiana</i> <i>A. amabilis</i>	<i>T. mertensiana</i> <i>A. amabilis</i> <i>C. nootkatensis</i>	<i>V. alaskaense</i> <i>V. membranaceum</i>	Brooke et al. 1970
<i>T. mertensiana</i> / <i>Vaccinium</i> <i>membranaceum</i> P.C.	Mountains of British Columbia to central Oregon	Warm dry to well- drained	Seral to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. amabilis</i> <i>P. contorta</i> <i>P. engelmannii</i>	<i>V. membranaceum</i> <i>X. tenax</i> <i>P. secunda</i>	Brockway et al. 1983 Brooke et al. 1970 Franklin 1966
<i>T. mertensiana</i> - <i>A. amabilis</i> / <i>V. membranaceum</i> P.C.						

APPENDIX—Continued

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ^a
<i>Tsuga mertensiana</i> / <i>Vaccinium scoparium</i> P.C.	Mountains of central and northwestern Oregon	Cool dry	Seral or minor climax to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. magnifica</i> <i>P. monticola</i> <i>P. albicaulis</i> <i>P. contorta</i> <i>P. engelmannii</i> <i>A. amabilis</i> <i>A. procera</i>	<i>V. scoparium</i> <i>C. pensylvanica</i> <i>L. glabrata</i> <i>X. tenax</i> <i>V. membranaceum</i>	Hemstrom et al. 1982 Hopkins 1979 Volland 1976
<i>Tsuga mertensiana</i> / <i>Xerophyllum tenax</i> H.T.	Mountains of northern Idaho, northwestern Montana. Mountains of British Columbia south to central Oregon	Warm dry	Seral to or co-climax with <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. contorta</i> <i>P. menziesii</i> <i>P. engelmannii</i> <i>P. albicaulis</i> <i>P. monticola</i> <i>L. occidentalis</i>	<i>X. tenax</i> <i>V. membranaceum</i> <i>V. globulare</i>	Cooper et al. 1983 ^a Daubenmire and Daubenmire 1968 Pfister et al. 1977
<i>Tsuga mertensiana</i> / <i>Clintonia uniflora</i> H.T.	Mountains of northern Idaho	Warm moist	Seral or minor climax to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>P. contorta</i> <i>L. occidentalis</i>	<i>C. uniflora</i> <i>X. tenax</i> <i>M. ferruginea</i>	Cooper et al. 1983 ^a
<i>Tsuga mertensiana</i> / <i>Luzula hitchcockii</i> H.T.	Mountains of western Montana and northern Idaho	Cool well- drained	Co-climax with <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. contorta</i> <i>P. albicaulis</i> <i>P. engelmannii</i>	<i>L. hitchcockii</i> <i>V. scoparium</i> <i>X. tenax</i> <i>A. latifolia</i>	Pfister et al. 1977
<i>Tsuga mertensiana</i> / <i>Phyllodoce</i> <i>empetriformis</i> P.C.	Russian Peak, Klamath Mountains, California	Cool wet	Minor climax to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. engelmannii</i> (minor climax) <i>P. contorta</i> <i>P. monticola</i> <i>P. brewerana</i> <i>T. brevifolia</i> <i>A. concolor</i> <i>A. amabilis</i>	<i>P. empetriformis</i> <i>L. glandulosum</i> <i>Kalmia polifolia</i> <i>Pyrola picta</i>	Sawyer and Thornburgh 1977
<i>Tsuga mertensiana</i> / <i>Streptopus</i> <i>amplexifolius</i> H.T.	Mountains of northern Idaho	Warm moist	Seral or minor climax to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>P. engelmannii</i> <i>P. menziesii</i> <i>L. occidentalis</i>	<i>S. amplexifolius</i> <i>S. triangularis</i> <i>T. carolinensis</i> <i>M. ferruginea</i>	Cooper et al. 1983 ^a
<i>Tsuga mertensiana</i> / <i>Pyrola picta</i> P.C.	Russian Peak, Klamath Mountains, California	Cool moist	Minor climax to <i>T. mertensiana</i>	<i>T. mertensiana</i> <i>A. amabilis</i> <i>A. concolor</i> <i>P. monticola</i> <i>P. flexilis</i>	<i>P. picta</i> <i>C. umbellata</i> <i>Penstemon newberryi</i> <i>Arctostaphylos patula</i> <i>Arctostaphylos</i> <i>nevadensis</i>	Sawyer and Thornburgh 1977
<i>Pinus albicaulis</i> series						
<i>Pinus albicaulis</i> / <i>Vaccinium scoparium</i> H.T.	Mountains of northwestern Wyoming	Cool dry	Minor climax to <i>P. albicaulis</i> <i>P. contorta</i>	<i>P. albicaulis</i> <i>P. contorta</i> <i>P. engelmannii</i>	<i>V. scoparium</i> <i>A. cordifolia</i> <i>C. rossii</i>	Steele et al. 1983
<i>Pinus albicaulis</i> / <i>Calamagrostis</i> <i>rubescens</i> P.C.	Eastside Cascades, north-central Washington	Cool dry	Seral to <i>P. albicaulis</i>	<i>P. albicaulis</i> <i>P. engelmannii</i> <i>P. contorta</i>	<i>C. rubescens</i> <i>P. myrsinites</i> <i>V. scoparium</i>	Williams and Lillybridge 1983
<i>Pinus albicaulis</i> / <i>Carex rossii</i> H.T.	Mountains of northwestern Wyoming	Cool dry	Minor climax to <i>P. albicaulis</i>	<i>P. albicaulis</i> <i>P. contorta</i> <i>P. engelmannii</i> (minor climax)	<i>C. rossii</i>	Steele et al. 1983
<i>Pinus albicaulis</i> - <i>Abies lasiocarpa</i> H.T.	Mountains of northern Idaho	Cool dry	Co-climax with <i>P. albicaulis</i>	<i>P. albicaulis</i> <i>P. engelmannii</i>	<i>V. scoparium</i> <i>A. latifolia</i> <i>Hieracium gracile</i>	Cooper et al. 1983 ^a Pfister et al. 1977

Habitat type, community type, plant community	Location	Site	Successional status of <i>A. lasiocarpa</i>	Principal tree associates	Principal understory species	Authority ¹
<i>Larix lyallii</i> series						
<i>Larix lyallii</i> - <i>Abies lasiocarpa</i> H.T.	Mountains of Montana west of Continental Divide	Cool dry	Co-climax with <i>L. lyallii</i>	<i>L. lyallii</i> <i>P. engelmannii</i> <i>P. contorta</i>	<i>P. empetrifloris</i> <i>V. scoparium</i> <i>L. hitchcockii</i>	Cooper et al. 1983 ⁴ Pfister et al. 1977
<i>Larix lyallii</i> / P.C.	Eastside Cascades, north-central Washington	Cool dry	Seral to <i>L. lyallii</i>	<i>L. lyallii</i> <i>P. engelmannii</i> <i>P. albicaulis</i>	<i>Cassiope</i> spp. <i>V. scoparium</i> <i>P. empetrifloris</i>	Williams and Lillybridge 1983
<i>Chamaecyparis nootkatensis</i> series						
<i>Chamaecyparis</i> <i>nootkatensis</i> / <i>Rhododendron</i> <i>albiflorum</i> P.C.	Cascades, southern Washington and northern Oregon	Cool wet	Seral to <i>C. nootkatensis</i>	<i>C. nootkatensis</i> <i>T. mertensiana</i> <i>P. menziesii</i> <i>P. engelmannii</i> <i>A. amabilis</i>	<i>R. albiflorum</i> <i>Vaccinium ovalifolium</i> <i>V. membranaceum</i>	Franklin 1966
<i>Chamaecyparis</i> <i>nootkatensis</i> / <i>Lysichitum</i> <i>americanum</i> P.C.	Mountains of southern British Columbia	Cool wet	Seral to <i>C. nootkatensis</i>	<i>C. nootkatensis</i> <i>T. mertensiana</i> <i>P. engelmannii</i> <i>A. amabilis</i>	<i>L. americanum</i> <i>Coptis asplenifolia</i> <i>O. horridum</i>	Brooke et al. 1970

¹Alexander, Billy G., Jr., E. Lee Fitzhugh, Frank Ronco, Jr., and John A. Ludwig. 1984b. A classification of forest habitat types of the Cibola National Forest, New Mexico. Draft of manuscript in preparation.

²Youngblood, Andrew P. 1984. Coniferous forest habitats of central and southern Utah. Draft of manuscript in preparation.

³Steen, Ordell, and Ralph Dix. 1974. A preliminary classification of Colorado subalpine forests. Unpublished report, 10 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

⁴Cooper, Steven, Kenneth Nieman, and Robert Steele. 1983. Forest habitat types of northern Idaho. Unpublished Report, 210 p. Intermountain Forest and Range Experiment Station, Ogden, Utah, and Northern Rocky Mountain Region, Missoula, Mont.

⁵Hess, Karl, and Clinton H. Wasser. 1982. Grassland, shrubland and forestland habitat types on the White River and Arapaho National Forests. Final Report, 335 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

⁶DeVelice, Robert L., John A. Ludwig, William H. Moir, and Frank Ronco, Jr. 1984. A classification of forest habitats in northern New Mexico and southern Colorado. Draft of manuscript in preparation.

⁷Fitzhugh, E. Lee, William H. Moir, John A. Ludwig, and Frank Ronco, Jr. 1984. Forest habitat types on the Apache, Gila and part of Cibola National Forests. Draft of manuscript in preparation.

⁸Komarkova, Vera. 1984. Habitat types on selected parts of the Gunnison and Uncompahgre National Forests. Preliminary Report, 254 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Alexander, Robert R., Raymond C. Shearer, and Wayne D. Shepperd. 1984. Silvical characteristics of subalpine fir. USDA Forest Service General Technical Report RM-115, 29 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

This report summarizes information on distribution, botanical description, habitat conditions, life history, special uses, and genetics of subalpine fir.

Keywords: Silvical characteristics, silvics, *Abies lasiocarpa*

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Plains

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Rocky Mountain Forest and Range Experiment Station

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